

REVISION OF THE GENUS DAHLIA
(COMPOSITAE, HELIANTHEAE — COREOPSIDINAE)

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The genus *Dahlia* (Compositae, Heliantheae — Coreopsidinae) famed because of its numerous ornamental forms of gardens, was named by Cavanilles in 1791 honoring Andreas Dahl, a Swedish botanist and pupil of Linnaeus. It is composed of four sections, twenty-seven species, and four infraspecific taxa and is largely restricted to the highlands (1500-4300 meters elevation) of México and Central America. Two species, *Dahlia coccinea* and *D. imperialis*, are also found in some countries of South America where they are believed to have been introduced. The genus encompasses some extremely diverse life forms ranging from dwarfed perennial herbs scarcely over four decimeters tall (*D. scapigera*) to huge arborescent plants which, in some instances, ascend to eight or nine meters (*D. imperialis*), and to scrambling epiphytic vines which sprawl among the tree-tops in rain forest (*D. macdougalii*). The great majority of the species have extremely restricted ranges, but one (*D. coccinea*) may be considered a roadside weed and is very wide-ranging throughout México and Guatemala.

Most historical accounts of the genus *Dahlia* have dealt with its rather important role in horticulture. Little or no attention has been given the fact that the genus is composed first of all of a group of wild species some of which have served as the progenitors of our garden subjects. Similarly workers who have written about the wild species have seldom taken into account the aspects of the genus in horticulture. As is discussed in detail later in this work, there appear to be just two of the naturally occurring species of *Dahlia* which have been involved, through processes of hybridization and selection, in the production of the numerous garden forms now known in cultivation the world over. In the past many hybrid variants were singled out and erroneously given formal taxonomic rank and provided with

Latin names, often also with Latin and vernacular diagnoses. Such treatment of these cultivars has given them the semblance of being botanical species. The purpose of the present study is to direct attention primarily to the systematics of the wild species where they occur naturally, while borrowing from the horticultural literature such names and information as are appropriate in clearing up misunderstandings in nomenclature. Elsewhere I shall present a full exploration of the history of *Dahlia* from the viewpoint of its cultivation dealing at length with its role in horticulture.

The formal history of *Dahlia* begins in the late 18th Century in Spain when Antonio José Cavanilles described and illustrated *Dahlia pinnata* in volume one of his *Icones et Descriptiones Plantarum*, 1791. Cavanilles, then a senior member of the staff of the Royal Botanic Garden in Madrid (not the director as has so often been repeated in articles on *Dahlia*, see Colmeiro, 1875), had received seeds of Mexican plants from Vicente Cervantes, a botanist at the Mexican Botanic Gardens in the city of México. Plants grown from these seeds were cultivated in Madrid and they formed the basis of the material used by Cavanilles to prepare the six volumes of his *Icones* issued during the years 1791-1801. Among these seeds were those of the original *Dahlia pinnata* as well as some of two additional species, *D. rosea* and *D. coccinea* which Cavanilles subsequently described in volume three of the *Icones*, 1796. Thus from the beginning Dahlias have been plants of gardens.

During the 17th and 18th centuries Europeans had a lively interest in the plants being brought back from the New World and botanical institutions freely exchanged seeds of noteworthy introductions. In this atmosphere Dahlias were, within a matter of a few years, found in the major botanic gardens of France, Italy, Germany and England. Presumably the earliest source of these plants was Madrid whence the gardens of France and England received their seeds, but meanwhile other plant collectors had also introduced *Dahlia* seeds into Europe from México. In any case, it is clear by the large numbers of variants which arose

among the plants in their gardens that Dahlias were creating a mild sensation among European horticulturists of the time.

Willdenow was the first to present a generic treatment of *Dahlia*. In his ed. 4 of *Linneaus' Species Plantarum*, 1803, he included the three species described by Cavanilles but he adopted in place of *Dahlia*, the name *Georgina* believing that *Dahlia* Cav. was preoccupied by *Dahlia* Thunberg (1792) of the Hamamelidaceae for which Persoon subsequently substituted the name *Trichocladus*. Although *Georgina* eventually came to be widely used, and is today a vernacular name for the garden Dahlia in Scandinavia and the countries east of the Rhine, botanists of the time mostly recognized Willdenow's error in dates and continued to publish notices, using the name *Dahlia*. In 1804, Thouin, working from material of the genus under cultivation in the gardens of the Paris Natural History Museum, published what must be taken as the first treatise on the cultivation of *Dahlia*. At the same time he offered a brief taxonomic review of the species accompanied by the world's first published colored portrait of them. This portrait must have caused considerable interest because almost at once it was reproduced in several gardening journals of the period and undoubtedly helped to create further enthusiasm for these new garden plants. Willdenow, in 1809, again revised his classification of *Georgina* recognizing two species. One of his species was given the aptly chosen name *G. variabilis* under which he placed all of the cultivated forms with ligules of purple, lilac, or rosaceous colors. For these he gave the varietal names of *purpurea*, *lilacina*, and *pallida*. Similarly, he placed all of the scarlet, orange, and yellow-rayed forms under *G. coccinea* and provided the corresponding varieties *coccinea*, *crocea*, and *flava*. One can appreciate Willdenow's problem as the number of Dahlias developed in gardens created an ever-increasing and bewildering array of new and different forms. The name *variabilis* seemed to fit the garden Dahlia so well that it was immediately adopted almost to the exclusion of all others.

The following year, 1810, de Candolle, seemingly in deference to the lead established by Willdenow, published a revision of *Dahlia* under the name *Georgina*. This paper appeared in the Annals of the Paris Natural History Museum whose editors added a disclaimer stating they were publishing the paper just as de Candolle requested despite their feeling that the name *Dahlia* should have been used. The generic treatment offered by de Candolle is very similar to that of Willdenow on the infraspecific level but for *G. variabilis* Willd. he substituted *G. superflua* and for *G. coccinea* (Cav.) Willd., *G. frustranea*. These new names had a brief acceptance but de Candolle himself even submerged them in the synonymy of his treatment of *Dahlia* for the *Prodromus* (1836). In 1829, Desfontaines offered in his ed. 3 of the *Catalogus Plantarum Horti Regii Parisiensis*, the combination *Dahlia variabilis* (Willd.) Desf. in the synonymy of which he placed Willdenow's *Georgina variabilis* and de Candolle's *G. superflua*. Since that time, *Dahlia variabilis* has become widely used and persists even in current literature as the name for the cultivated garden Dahlia.

During the remainder of the 19th and in the early years of the 20th centuries, several more species of *Dahlia* were described. A good summary of the taxonomy and nomenclature of the genus was offered by Hemsley in 1879 and again in 1881. Between the time of Hemsley and the present the greatest contributions to our understanding of the wild *Dahlia* species came from the work of E. E. Sherff who, at the time of his death, April 1966, was regarded as a leading authority on this and other genera of the Compositae. In 1930, in connection with his monographic work on the Compositae, Subtribe Coreopsidinae, Sherff described *D. linearis* and thereafter regularly published notes including descriptions of several more new taxa until, in 1955, for an installment of the *North American Flora*, he contributed the most recent systematic treatment of the genus. Here he recognized 29 taxa, including 18 species, 8 varieties, and 3 forms. In the present treatment, one section, six species, and two varieties are proposed as new. Of the 29 taxa recog-

nized by Sherff 12 are maintained here, six are reduced to synonymy and ten are recombined at different taxonomic levels.

Table 1. Conspectus of the species and summary of chromosome numbers of the Genus *Dahlia*.

Section 1. Pseudodendron Sherff	
1. <i>D. excelsa</i> Benth.	
2. <i>D. imperialis</i> Roezl ex Ortgies	($n = 16$)
3. <i>D. tenuicaulis</i> Sorensen, sp. nov.	($n = 16$)
Section 2. Epiphytum Sherff	
4. <i>D. macdougallii</i> Sherff	
Section 3. Entemophyllon Sorensen, sect. nov.	
5. <i>D. scapigeroides</i> Sherff	
6. <i>D. foeniculifolia</i> Sherff	
7. <i>D. linearis</i> Sherff	($n = 17$)
8. <i>D. rupicola</i> Sorensen, sp. nov.	($n = 17$)
9. <i>D. dissecta</i> S. Wats	
9a. var. <i>dissecta</i>	($n = 17$)
9b. var. <i>sublignosa</i> Sorensen, var. nov.	
Section 4. Dahlia	
10. <i>D. merckii</i> Lehm.	($n = 18$)
11. <i>D. apiculata</i> (Sherff) Sorensen, comb. & stat. nov.	
12. <i>D. cardiophylla</i> Blake & Sherff	($n = 16$)
13. <i>D. purpusii</i> Brandg.	
14. <i>D. pinnata</i> Cav.	($n = 32$)
15. <i>D. pteropoda</i> Sherff	
16. <i>D. brevis</i> Sorensen, nom. nov.	($n = 16$)
17. <i>D. rudis</i> Sorensen, sp. nov.	
18. <i>D. moorei</i> Sherff	
19. <i>D. hintonii</i> Sherff	
20. <i>D. mollis</i> Sorensen, sp. nov.	($n = 16$)
21. <i>D. atropurpurea</i> Sorensen, sp. nov.	($n = 32$)
22. <i>D. australis</i> (Sherff) Sorensen, comb. & stat. nov.	
22a. var. <i>australis</i>	($n = 16$ & 32)
22b. var. <i>liebmannii</i> (Sherff) Sorensen, comb. nov.	
22c. var. <i>chiapensis</i> Sorensen, var. nov.	
22d. var. <i>serrator</i> (Sherff) Sorensen, comb. & stat. nov.	

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|---|------------------|
| 23. <i>D. sherffii</i> Sorensen, sp. nov. | ($n = 32$) |
| 24. <i>D. scapigera</i> (A. Dietr.)
Knowles & Westc. | ($n = 16$) |
| 25. <i>D. barkerae</i> Knowles & Westc. | ($n = 32$) |
| 26. <i>D. tenuis</i> Robinson & Greenman | ($n = 16$) |
| 27. <i>D. coccinea</i> Cav. | ($n = 16$ & 32) |

Evidence supporting the taxonomic and nomenclatural changes herein proposed for the genus *Dahlia* has been gathered from three main avenues of research: field studies of the intra- and interpopulational variability, morphologic studies using both living materials and herbarium specimens, and chromosomal studies. Pertinent data are discussed where appropriate in connection with the taxonomic treatment of the species to which they apply. However, it is useful at this point to offer a brief explanation of the mode of morphologic variability found among the species and to call attention to certain features of the foliage and the terminology used. Also, for the purposes of the present treatment, the principal details of the chromosomal studies are outlined below. A full report on this phase of the research will be presented elsewhere.

Chromosomal Studies

Chromosome numbers are now known for 17 taxa of the genus *Dahlia* as follows (see also Table 1):

$n = 16$	7 spp.
$n = 17$	3 spp.
$n = 18$	1 sp.
$n = 16$ & 32	2 spp.

Ishikawa (1911) was the first to publish a report on *Dahlia* chromosomes. He found the numbers of *D. variabilis* (i.e., *D. pinnata*) and *D. coronata* (i.e., *D. coccinea*) to be $2n = 64$ and 32 respectively. *Dahlia imperialis* was reported to have 32 ($n = 16$) chromosomes by Belling (1924) and in 1929 Lawrence added a report on *D. merckii* ($n = 18$). Thus, at the outset of this study, three of the four numbers found in the genus were known. The fourth,

$n = 17$ (*D. dissecta*,¹ *D. linearis*, and *D. rupicola*), is reported here for the first time.

Several interesting remarks may be made concerning the distribution of chromosome numbers within *Dahlia*. In some instances the chromosome numbers correlate remarkably with morphologic data. This is demonstrated particularly well among the taxa of the newly described section Entemophyllon which on morphologic grounds are clearly allied. All are diploids and all have the same chromosome number, $n = 17$. Moreover, the aneuploid *D. merckii*, $n = 18$, comes morphologically closest to the members of this section. Similarly, the two species of "tree-dahlias" of section Pseudodendron are diploids and share the same chromosome number, $n = 16$. The only tetraploids ($n = 32$) known in the genus occur within the section Dahlia where they number about as many as the diploids. Two of the species, *D. coccinea* and *D. australis*, are composed of both diploid and tetraploid races. A majority of the species have rather restricted geographic ranges and it is significant that most of these are diploids. Notable exceptions are *D. merckii* and *D. coccinea* which are rather wide ranging though the tetraploid races of *D. coccinea* extend over a much greater area than do the diploid.

Morphological Considerations

The size, shape, and segmentation of the compound leaves of some *Dahlia* species are extremely variable. To promote clarity in the use and understanding of the keys and descriptions a brief explanation is provided below of the type of materials, the technical characters, and the terminology employed in the systematic treatment. It is hoped that this will also serve as a guide to the type of materials one should gather when making future collections of *Dahlia*.

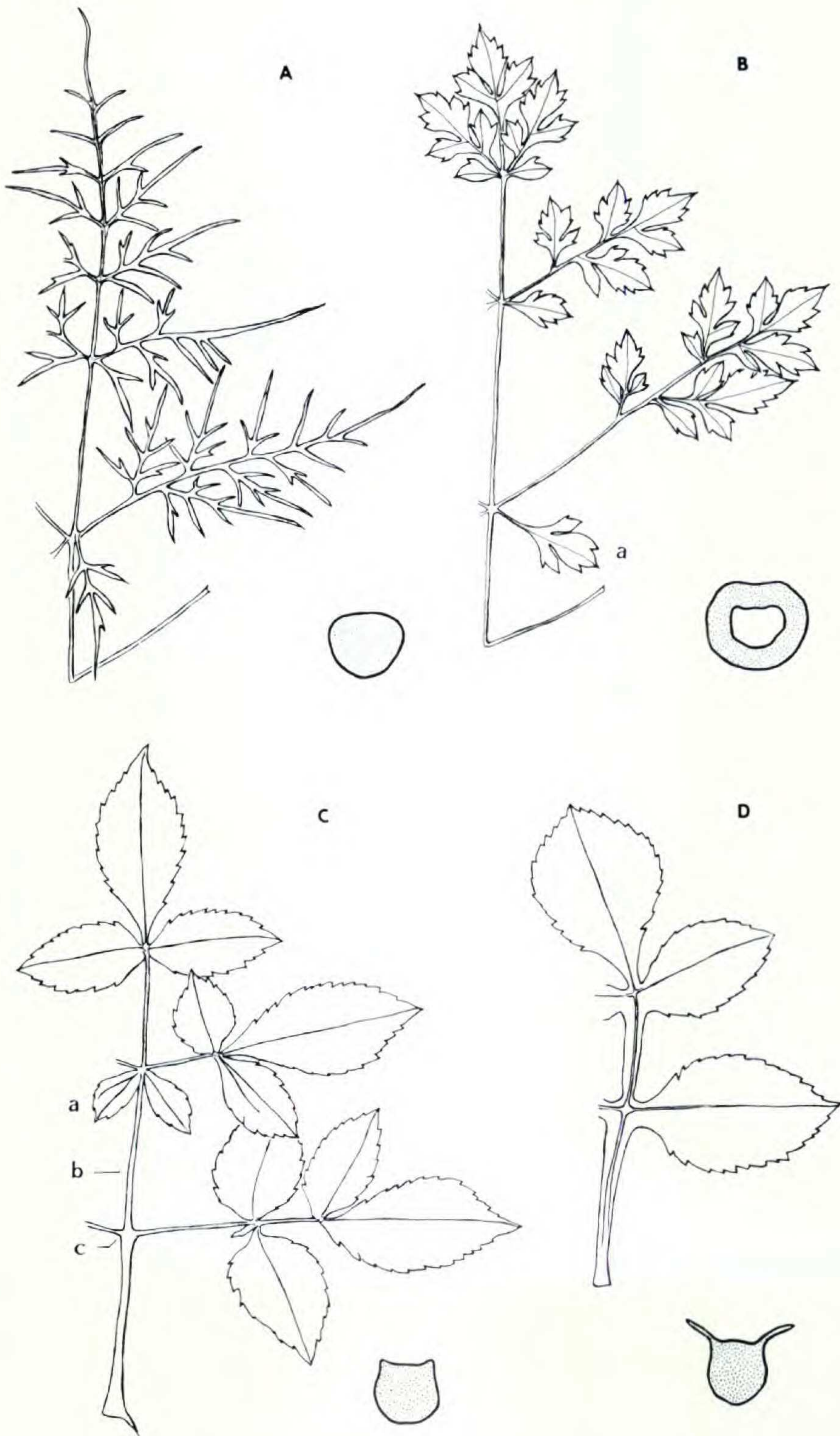
- a) All descriptions of the species are based upon data derived from mature plants collected in the field, not greenhouse-grown individuals. The latter often

¹A previous report (Turner *et.al.*, 1962) of the chromosome number of *D. dissecta* as $n = 18$ was based on a specimen (*Rock M-351* [TEX]) of *D. merckii*.

exhibit altered characters such as smaller leaf segments and longer petioles. Plants in their first year of growth from seed usually produce juvenile foliage unlike that on the same individual grown from tubers in later years.

- b) Measurements of stems and leaves are based on *median* leaves and adjacent portions of the stems.
- c) Length of leaves includes the petiole and terminal leaflet.
- d) Width of leaves is measured at the basal pair of leaflets or lobes.
- e) Length of leaflets is based solely on the *basal* pinna and is measured from the primary rachis to the tip of the terminal pinnule. In the same manner, the length of pinnules is measured from the rachilla to the tip of the basal pinnule on that axis. The necessity of designating, in this way, precisely which portion of the leaf is being measured is seen from the selected types of leaves portrayed in Fig. 1. Note that the basal pinna and pinnules are always the largest and that they diminish greatly in size the more distal they are.
- f) Shapes of leaflets are of the blades of ultimate segments as, for example, in the case of bipinnate leaves, the basal pinnule of the basal pinna. Exceptions to this occur in some descriptions when specific reference is made to another segment such as the terminal leaflet or terminal pinnule.
- g) The petiole is measured from the stem to the junction of the basal pair of leaflets. In the case of pinna-

Fig. 1. Selected leaf types $\times \frac{1}{2}$ and their corresponding petiolar cross-sections $\times 2$ of *Dahlia* spp. A. a compound leaf with alternate pinnules, *Dahlia rupicola*; B. a compound leaf with alternate pinnules, *Dahlia merckii*; C. a compound leaf with opposite pinnules, from an artificial hybrid, *Dahlia australis* var. *australis* \times *coccinea*; D. a pinnatissect leaf, *Dahlia pinnata*; a. *stipel*, note the compound stipels on the leaf of A; b. *rachis internode*; c. *rachis node*.



tifid leaves (Fig.1-D) when the limits of the petiole are not clear, measurements are from the stem to the junction of the first (i.e. basal or proximal) pair of main lateral veins. Petiolules and pseudopetiolules are measured in the same way.

- h) Petiolar cross-sections are taken from a point midway between the stem and basal pair of leaflets or main lateral veins. Types encountered are shown in Fig. 1. If working with dried material it is possible to see clearly all the diagnostic features of these cross-sections following hydration in warm water.
- i) The junction of the primary rachis with the secondary rachis or rachilla is termed a "rachis node". Consequently, a "rachis internode" denotes the portion of the axis between the junctions of successive pairs of leaflets (see Fig. 1).
- j) The leaves of various species within *Dahlia* may be sorted into four main classes: simple leaves, compound leaves with alternate pinnules (Fig. 1-A, & -B), compound leaves with opposite pinnules (Fig. 1-C), and pinnatifid or pinnatisect leaves (Fig. 1-D). The degree of dissection of compound leaves, whether once-pinnate, bi-, or tri-pinnate, has been based solely on the basal pinnae.
- k) The occurrence of *stipels*, as seen in the leaves of Fig. 1-A, -B, & -C) is diagnostic with some species and not so with others. Attention is being called to them so the user may be aware of the structure to which the term refers.
- l) The principal diagnostic features of the heads are the rays (for their color) and the outer whorl of involucral bracts (for their position, size, shape, and ornamentation). In all cases, the character-

istics of these structures are based on heads in anthesis.

The nature of the materials needed for the identification of most *Dahlia* species is implicit in the foregoing notes. However, the species of the section *Pseudodendron*, the so-called "tree-dahlias", require special mention. Most leaves of these species are too large to collect intact. A single leaf may measure 80 to 90 centimeters long. Collectors should select a single basal pinna of a median leaf and supplement the specimen with notes on total length of the leaves and the number of primary leaflets. Notes should also be made concerning the height and habit of the plants. Collections of the suffrutescent species should include a portion of the two-year-old stem.

Various authors and collectors have, at times, confused species of *Dahlia* and *Cosmos*. This has been particularly true of *Cosmos diversifolius* which is easily mistaken for *Dahlia scapigera*, and *D. brevis* which has been identified as *Cosmos concolor*. At anthesis *Cosmos* species are distinguished by a cylindrical brush of hairs on each of the five staminal filaments, while in species of *Dahlia* the filaments are smooth. In fruit the achenes of *Dahlia* are obcompressed and mostly 2-sided or slightly 3-angled in cross-section, those of *Cosmos*, quadrangular. The fleshy outer involucre bracts of *Dahlia*, especially as seen in fresh material, are quite distinct from the thin bracts of *Cosmos*. Species of the closely allied and deceptively similar *Hidalgoa*, often called climbing-dahlia, are distinguished by their sterile disc florets, and their petioles which twist and cling in the manner of *Clematis*.

I cannot conclude this introduction without acknowledging with sincere thanks the help of many persons — Dr. Thomas E. Melchert, University of Iowa, for suggesting the study and guiding me from its beginning; Dr. George W. Martin, Professor Emeritus, for his advice and encouragement over the years; Daniel J. Crawford, for his companionship in the field in México and assistance with other phases of

the research; Dr. Jerzy Rzedowski, Curator of the Herbarium, Instituto Politécnico Nacional, México, D. F., for his help with locating many obscure place names in México and his advice on highway travel in that country. Many thanks are due the staff of the Arnold Arboretum, Dr. Richard A. Howard, Director, Dr. Carroll E. Wood, Jr., Dr. Bernice Schubert, and Dr. Gordon P. DeWolf, Jr., who critically read the manuscript and offered many helpful suggestions in nomenclatural and editorial matters.

During two field trips through México and Central America I was able to collect 18 of the 31 taxa recognized here. In addition to recollecting many poorly known species and making extensive observations of natural populations, I was able to gather propagating materials of species which had never before been brought under cultivation. Being able to observe living materials of the species pass through their life cycle greatly added to my present understanding of the genus. The study is otherwise based on herbarium specimens borrowed from the following institutions (the standard abbreviations of Index Herbariorum are used consistently throughout this work) :

A	Arnold Arboretum, Harvard University
BH	Bailey Hortorium, Cornell University
CAS	California Academy of Sciences
DS	Dudley Herbarium, Stanford University
F	Field Museum of Natural History
GH	Gray Herbarium, Harvard University
IA	The University of Iowa
ISC	Iowa State University
MEXU	Herbario Nacional, Instituto de Biología, Universidad Nacional de México
MICH	University of Michigan
MSC	Michigan State University
MO	Missouri Botanical Garden
NY	New York Botanical Garden
POM	Pomona College
RSA	Rancho Santa Ana Botanic Garden
TEX	University of Texas

UC	University of California
US	U. S. National Herbarium, Smithsonian Institution
WIS	University of Wisconsin

I am grateful to the curators of these herbaria for the loan of specimens. I should like also to acknowledge the assistance of the National Science Foundation whose grant (No. GB-3851) to Dr. Thomas E. Melchert helped to defray the expenses of the field work.

Specimens cited in the lists of exsiccatae are arranged in a geographic sequence by country from east to west. The states of México are in order more or less by tier from north to south and within each tier from east to west. A complete first set of my own collections from México and Guatemala is on deposit at IA.

SYSTEMATIC TREATMENT

Dahlia Cav. *Icones et Descr. Pl.* 1: 56. 1791. Type species: *Dahlia pinnata* Cav. (see Sherff, 1955.)

Georgina Willd., *Linn. Sp. Pl. ed. 4. 3:* 2124. 1803. Type species: *Georgina purpurea* Willd.

Georgia Sprengel, *Anleitung zur Kenntniss der Gewächs*e, ed. 2. 2: 567. 1818. Type species: *Georgia variabilis* Willd.

Scrambling epiphytes, herbaceous or suffrutescent perennials, developing from fascicled tubers or with the rootstock tuberously thickened, in one epiphytic species the roots aërial (*D. macdougalii*). Stems erect, rarely vine-like, arising singly (sect. *Dahlia*), 2-4 (sect. *Pseudodendron*), or many in a cluster (sect. *Entemophyllon*), the individual stems mostly unbranched except in the flowering portion or branching freely from the base (*D. merckii*); internodes hollow or solid, sometimes the pith chambered (sect. *Entemophyllon*); nodes septate or the septa sometimes incomplete. Leaves opposite or whorled (3 per node); simple to 3-pinnately compound, often stipellate; margins ciliolate or eciliolate. Heads radiate, on long, slender, naked peduncles; involucral bracts distinctly bi-seriate, the outer (4-)5(-6-7) erect, spreading or reflexed at anthesis, fleshy, dorsally several-lined, green, narrowly linear to broadly ovate or obovate, the inner (7-)8(-9), membranous, many-lined, variously tan, red, reddish-brown or brown, often the tips colored purple or red, margins scarious or white-hyaline, ovate, subacute, obtuse, or emarginate, enlarging in fruit

to about twice their size at anthesis; chaff scarious, light tan suffused with red or purple, resembling the inner bracts but with fewer lines, subtending each disc floret, ovate, obtuse or subacute; ray florets neutral or pistillate sterile, rays white or whitish-lavender to deep purple or yellow to various shades of orange to deep blackish-scarlet, narrowly or broadly ovate, acute, often minutely denticulate, sometimes the veins dorsally minutely pubescent; disc florets yellow, yellow with red or purple tips or the limb purple throughout, 17-172 per head, hermaphrodite, fertile, tubular (all or some replaced by sterile or fertile ligulate florets in many horticultural forms), corolla expanded into a 5-toothed, cylindrical limb, the teeth erect, spreading, recurved or strongly revolute; filaments glabrous; style branches linear-lanceolate, bearded dorsally for $\frac{3}{4}$ their length, ventrally near the tips only, spreading or slightly reflexed at anthesis. Achenes grayish-black to black at maturity, more or less linear to linear-oblongate, rarely broadly spatulate, obcompressed, obscurely sulcate, sometimes puberulent (minutely tuberculate in sect. *Entemophyllon*), often slightly constricted just beneath summit and capped by a shallow tan disc (or the disc swollen and black in *D. moorei*); pappus obsolete or consisting of 2 minute rudiments, these sometimes elongated to 1 mm., rarely greatly elongated into weak, flexuous filiform, often caducous, threads. Chromosome numbers, $n = 16, 17, 18,$ and 32 .

KEY TO THE SECTIONS

- A. Plants liana-like, producing aërial roots to 22 m. long; stems scrambling for great distances in the tree tops of rain forest west of Tehuantepec. Sect. 2. Epiphytum.
- A. Plants growing erect, not vine-like; roots tuberous and anchored in the soil, not aërial.
 - B. Plants suffrutescent, 21-90 dm. tall; ligneous stems of the previous year 1.5-10 cm. diam.; pinnules opposite on the rachilla. Sect. 1. Pseudodendron.
 - B. Plants herbaceous, 4-30 dm. tall or subshrubs 9-15 dm. tall, if the latter, then the ligneous stems of the previous year 0.3-2 cm. diam.; pinnules opposite or alternate on the rachilla.
 - C. Pinnules or pinnular segments invariably alternate on the rachilla; petioles solid; leaves bipinnatisect to bipinnate-pinnatisect. Sect. 3. Entemophyllon.
 - C. Pinnules or pinnular segments opposite on the rachilla or if alternate then the petiole hollow or the leaves merely simple. Sect. 4. Dahlia.

KEY TO THE SPECIES

Section 1. Pseudodendron

- A. Principal leaves 50-90 cm. long

- B. Primary pinnae 3-7; outer involucral bracts linear. 1. *D. excelsa*.
- B. Primary pinnae 9-15; outer involucral bracts obovate or oblanceolate. 2. *D. imperialis*.
- A. Principal leaves 20-43 cm. long. 3. *D. tenuicaulis*.

Section 2. Epiphytum

- One species. 4. *D. macdougalii*.

Section 3. Entemophyllon

- A. Outer involucral bracts 5-9 mm. long; petioles solid.
 - B. Peduncles 1.5-10 cm. long; outer bracts acute; current year's growth developing from woody stems, these usually with chambered pith. 7 *D. linearis*.
 - B. Peduncles 12-37 cm. long; outer bracts obtuse or subacute; plants herbaceous or with short (5-15 cm.) lengths of the previous year's stems becoming slightly woody, sometimes with chambered pith.
 - C. Plants herbaceous; heads 3.5-6 cm. diam. 9a. *D. dissecta* var. *dissecta*.
 - C. Plants subherbaceous, short (5-15 cm.) lengths of the previous year's stems becoming slightly woody (or with some stems herbaceous, having developed directly from the tuberous rootstock); heads 5.5-8.5 cm. diam. 9b. *D. dissecta* var. *sublignosa*.
- A. Outer involucral bracts 9-18 mm. long; petioles solid or hollow.
 - D. Stems living more than one season and branching to produce the current season's growth; petioles solid.
 - E. Ultimate segments or their lobes (whichever are narrower) of median leaves 0.5-3.2 mm. wide. 8. *D. rupicola*.
 - E. Ultimate segments of median leaves 5-16 mm. wide. 5. *D. scapigeroides*.
 - D. Stems living only one season, the current season's growth arising from a crown or tuberous rootstock beneath the soil; petioles solid or hollow.
 - F. Petioles solid. 6. *D. foeniculifolia*.
 - [F. Petioles hollow. 10. *D. merckii* (of Sect. 4. Dahlia)]

Section 4. Dahlia

- A. Outer involucral bracts reflexed at anthesis (sometimes merely spreading but not ascending).
 - B. Median leaves compound or if simple then the petiole more than 3 mm. long.
 - C. Rays white, whitish-lavender, light purple to dark blackish purple.
 - D. Current year's growth branching from ligneous stems of the previous year. 11. *D. apiculata*.

- D. Current year's growth from subterranean tubers or rootstock.
- E. Petioles broadly auriculate-winged at the base, 1-4.2 cm. wide, upper surface of leaves glabrous or essentially so, lower surface pilose or merely pubescent; stem 6-furrowed. 15. *D. pteropoda*.
- E. Petioles without wings or if winged then not forming broad auricles at the base.
- F. Leaves and stems densely soft pubescent, pilose on lower surfaces of leaves (hairs diminishing on branches of the inflorescence and on parts of the heads). 20. *D. mollis*.
- F. Leaves and stems not densely pubescent nor pilose.
- G. Outer involucral bracts flagelliform with long-attenuate tips, 10-17 mm. long, broadest at or near the base, 1.5-4 mm. wide; achenes 6-8 mm. long, constricted slightly below the summit to form a black disc less than 1 mm. wide and barely 0.4 mm. high. 18. *D. moorei*.
- G. Outer involucral bracts not long flagelliform, sometimes acuminate, but the tips not long attenuate, broadest at or beyond the middle.
- H. Outer involucral bracts 14-24 mm. long, dorsally glabrous.
- I. Rachis, petiole and petiolule usually winged; the terminal leaflet or segment with (11-)12-15 teeth per side; blades flexible when dry, surfaces not strongly bi-colored; outer bracts (4-)5-10 mm. wide. 17. *D. rudis*.
- I. Rachis, petiole and petiolule not conspicuously winged; the terminal leaflet or segment with 3-9(-11) teeth per side; leaflets brittle and stiff when dry, surfaces bi-colored, the lower usually lighter green; outer bracts 2-6 mm. wide. 22d. *D. australis* var. *serrator*.
- H. Outer involucral bracts 2-12(-14) mm. long, if longer then dorsally pilose.
- J. Petioles solid, more than 1.2 cm. long.
- K. Outer involucral bracts glabrous on the dorsal surface or with a few scattered hairs.
- L. Rays drying to dark blackish purple; outer bracts ventrally appressed pubescent; leaflets (ex-

- cept sometimes the terminal leaflet or segment) rounded at the base; hairs along the midrib beneath widely spaced, 12 or fewer per cm. 21. *D. atropurpurea*.
- L. Rays drying to rose or light purple.
- M. Leaves coarse textured, often scabrous, simple or more commonly pinnatisect to pinnate-pinnatisect; rachis, petiole and petiolule winged, often broadly so; margins coarsely toothed, the teeth protruding beyond the outline of the blades; basal pinna or lobe longer than the petiole.
..... 14. *D. pinnata*.
- M. Leaves upon drying becoming stiff but not coarse textured nor scabrous, 1- or 2- pinnate.
- N. Upper surface of leaves rugose, glabrous or a few scattered hairs near the apex, lower surface conspicuously lighter green or silvery green; margins revolute or obscurely so; native in Oaxaca, Chiapas and Guatemala.
..... 22. *D. australis*
incl. vars. *chiapensis* &
serrator.
- N. Upper surface of leaves smooth, not rugose, with scattered or broadly spaced antrorsely curved hairs and lines of very minute hairs following the main veins; lower surface not or but slightly lighter green; margins flat; native in Chihuahua, Durango and northern Zacatecas.
..... 23. *D. sherffii*.

- K. Outer involucral bracts copiously hairy or pilose on the dorsal surface. 19. *D. hintonii*.
- J. Petioles hollow or if solid then 0.8-1.2 cm. long.
 - O. Leaves (including petiole) 14-38 cm. long; petiole hollow, 4-16 cm. long. 10. *D. merckii*.
 - O. Leaves (including petiole) 5.5-8 cm. long; petiole solid, 0.8-1.2 cm. long. 22b. *D. australis* var. *liebmanii*.
- C. Rays yellow, orange, orange-scarlet or deep blackish scarlet.
 - P. Leaves (including petiole), 6-11 cm. long, pinnate-pinnatifid or pinnate-pinnatisect; plants 2.5-6 dm. tall; rays yellow. 26. *D. tenuis*.
 - P. Leaves (including petiole), 12-35 cm. long, simple to 3-pinnate; plants 4.5-30 dm. tall; rays yellow, orange, orange-scarlet or deep blackish scarlet. 27. *D. coccinea*.
- B. Median leaves simple, not lobed nor divided, sessile or the petioles 1-3 mm. long.
 - Q. Base of blade clasping the stem, the leaves sessile; margins with 5-8 teeth per side. 12. *D. cardiophylla*.
 - Q. Base of blade narrowed or rounded, the leaves sessile or short stalked, the petiole 1-3 mm. long; margins with 10-18 teeth per side. 13. *D. purpusii*.
- A. Outer involucral bracts erect or at least ascending at anthesis.
 - R. Leaves without stipels; outer bracts 4-7 mm. wide. 16. *D. brevis*.
 - R. Leaves usually with stipels present at the 1st and/or 2nd rachis node; outer bracts 1.8-3 mm. wide.
 - S. Outer bracts 6-6.5 mm. long; leaves (esp. on the under-surface and stems conspicuously hairy, the hairs shiny white, 2-5 mm. long, clearly multi-cellular; leaflets glossy dark green and rugose above. 25. *D. barkerae*.
 - S. Outer bracts 7-11 mm. long; leaves and stems glabrous or sparsely pubescent at the nodes on the stem and rachis, sometimes also dorsally along veins of leaflets; leaflets pale green and rugose above. 24. *D. scapigera*.

Section 1. Pseudodendron Sherff, Am. Jour. Bot. 38: 69. 1951. Type species: **Dahlia lehmannii** Hieron. (= *Dahlia imperialis* Roetzl ex Ortgies)

Suffrutescent perennials 2-6(-9) m. tall, stems becoming woody and often lasting more than one season, the older ones (1.5-)2-10 cm.

diam., internodes hollow, nodes strongly septate, leaves 1-, 2- or 3-pinnate, the principal ones 20-90 cm. long, apices of ultimate segments long attenuate, midveins tan colored beneath, heads obliquely erect or pendulous, numerous, rays white or whitish-lavender to light or rosaceous purple. (Species 1-3.)

1. **Dahlia excelsa** Benth. in Maund, Botanist. 2: pl. 88. 1838. TYPE: MEXICO: Valley of México (the exact locality not stated), 7 Oct. 1834, *William Bates s.n.* (Holotype: K; photo. of type: F!).

Dahlia excelsa var. *anemonaeflora* Benth. *Ibid.* Type: that of *D. excelsa* Benth.

Dahlia variabilis var. *excelsa* (Benth.) Walpers, Suppl. Prim. ad Rep. Bot. Syst. 2: 602. 1843. Type: that of *D. excelsa* Benth.

“Roots fascicled, some perennial, cylindrical, and fibrous, others swelling into tubers. STEM perennial, very thick, becoming woody, growing to the height of twenty feet and upwards, less branched, and assuming more the aspect of a tree than any other species, hollow inside, smooth and glaucous on the surface, marked with horizontal rings formed by the broad stem-clasping base of the petioles, and sometimes emitting near the base a great quantity of fibrous roots. LEAVES opposite, attaining the length of two feet and a half, by about two feet in breadth, doubly pinnatipartite, the general petioles broadly connate round the stem, the segments borne on sharp partial footstalks, those of the lower leaves ovate and heart-shaped at the base, those of the upper leaves, especially the end ones, often contracted at the base, acuminate, toothed, nearly smooth or with a few short scattered hairs, of a pale glaucous green underneath. FLOWER HEADS on long opposite monocephalous peduncles, collected five to eight together in a sort of corymb at the end of the branches, with occasionally a few axillary solitary ones along the stem. OUTER INVOLUCRE consisting of five or six linear spreading foliaceous squamae, the inner one of about twelve, oblong, obtuse, erect, membranous ones. FLORETS in the specimen we have seen all altered from their natural state, so as to give to the head of flowers the form known in other Dahlias by the name of anemone-flowered.

The florets of the ray appear to be nearly in their ordinary state, and to be naturally neutral and sterile, those of the disk are shorter but all converted into irregularly formed semi-ligulate sterile florets having lost their original colour to assume that of the ray. All traces of the organs of fructification are obliterated in all the florets."

The foregoing is quoted directly from Bentham (1838) who based his description of *Dahlia excelsa* on living specimens. For the present study the only material I have been able to examine are two photographs (housed at F) of the type specimens. Sherff (1951a) writes of having collected *Dahlia excelsa* in two places in Guatemala, September, 1949, under his numbers 5061, "Chichicastenango . . . garden at the south side of Santo Tomás church," and 5062, "roadside thicket above Sololá." In an effort to obtain additional specimens for study I revisited these localities, in the company of Dr. T. E. Melchert and Mr. D. J. Crawford, during late summer, 1966. Our search for this species was unsuccessful. At the garden of the Santo Tomás church we observed a large plant of *Dahlia imperialis*. It resembled the typical wild plants of that species we had seen in great numbers along roadsides in the general vicinity of Sololá earlier that day.

Later an effort was made to locate Sherff's collections of *Dahlia excelsa* referred to above. It was expected these would be deposited in the herbarium of the Field Museum in Chicago. Other *Dahlia* specimens were found there which Sherff had collected in Guatemala during the same trip, September, 1949, but his numbers 5061 and 5062 were not found. Nevertheless, I have assumed that Sherff did, in fact, have the benefit of additional material of *Dahlia excelsa* on which to base his amplified description which he offers of the species in North American Flora (Sherff, 1955). From his description the following salient features may be added to Bentham's original description given above:

". . . the larger leaves 6-7.5 dm. long including the glabrate petiole (this more or less 2 dm. long), 4-6 dm.

wide, their primary divisions (pinnae) each with but 1-5 leaflets (the terminal one often irregularly 2-3-parted), . . . margins coarsely serrate (with up to 21 teeth on a side), . . . ultimate segments to 1.7 dm. long and about 7 cm. wide; flowering heads . . . about 9 cm. across, . . . outer involcral bracts 5 or 6, linear . . . ligules lilac, oblong, about 3.5 cm. long, about 1.5 cm wide, . . . achenes not seen."

Valley of México (?) southeastward to southwestern Guatemala above Sololá.

In addition to the problem of the identity of *Dahlia excelsa* there is the question of the place of origin of the type. Bentham (1838) writes, "The Dahlias are all native in the mountainous districts of México, where the present species *Dahlia excelsa* had probably been discovered some years ago, as it appears to have long been cultivated in the Botanic Garden of the City of México." As seen in its photograph, the type in the Hooker Herbarium (K) bears a handwritten label stating the plant was collected in the Valley of México, but there is no mention on the label of a botanic garden. One wonders, therefore, how Bentham could have known about its having "long been cultivated in the Botanic Garden of the City of México," except had not William Bates, the collector, so informed him. Although it is not specifically stated, the indication is that the original material was collected by Bates in a Botanic Garden and he, perhaps assuming the plant had been introduced from nearby mountains, merely noted on the label the "valley of México." Certainly this region of México is botanically the best-known in that country, yet no specimens from this area, of *Dahlia excelsa* or any other "tree-dahlia," have been seen, except two specimens of *Dahlia imperialis* which have come from contemporary gardens.

On the characteristics displayed in the photographs of the type, *Dahlia excelsa* may be distinguished from *Dahlia imperialis* by its 3-7 (not 9-15) primary leaflets and from the new *Dahlia tenuicaulis* by the overall length of its leaves, "6-7.5 dm. long including the . . . petiole" (not 20-43

cm. long). Despite these distinctions and despite the unfortunate lack of material by which to judge, I strongly feel that *Dahlia excelsa* and *Dahlia imperialis* are variants of the same species. Nevertheless, I have chosen to retain *Dahlia excelsa* in the present treatment on a provisional basis.

2. ***Dahlia imperialis*** Roezl ex Ortgies in Regel, *Gartenflora* 12: 243. 1863. TYPE: exact place and date of collection not known; the plants collected in México by Roezl, brought to Zurich where cultivated, then to Berlin, the Royal Botanic Gardens, where cultivated and described, *Roezl s.n.* (Holotype: B[?]).

Dahlia arborea Hort. ex Regel, *Cat. Pl. Horti Aksakoviano* 1860. *nomen nudum.*

Dahlia maximiliana Hort. ex Hooker f. *Bot. Mag. pl.* 7655. 1899. This name also used in *Gard. Chron.* II. 11: 216 & 12: 525. 1879, but without adequate description. Lectotype: *pl.* 7655, Hooker f. *loc. cit.*

Dahlia lehmannii Hieron. *Bot. Jahrb.* 19: 55. 1894. Type: *Lehmann* 4894, Colombia (Holotype: B[?]; Isotype: F!).

Dahlia dumicola Klatt, *Bot. Beibl. zur Leopoldina* 6. 1895 & *Bull. Soc. Bot. Belg.* 35: 289. 1896. Lectotype: *Pittier & Tondue* 8469, Costa Rica (F!).

Dahlia maxonii Safford, *Jour. Washington Acad.* 9: 371. 1919. Type: *Maxon & Hay* 3295, Alta Verapaz, Guatemala (US!).

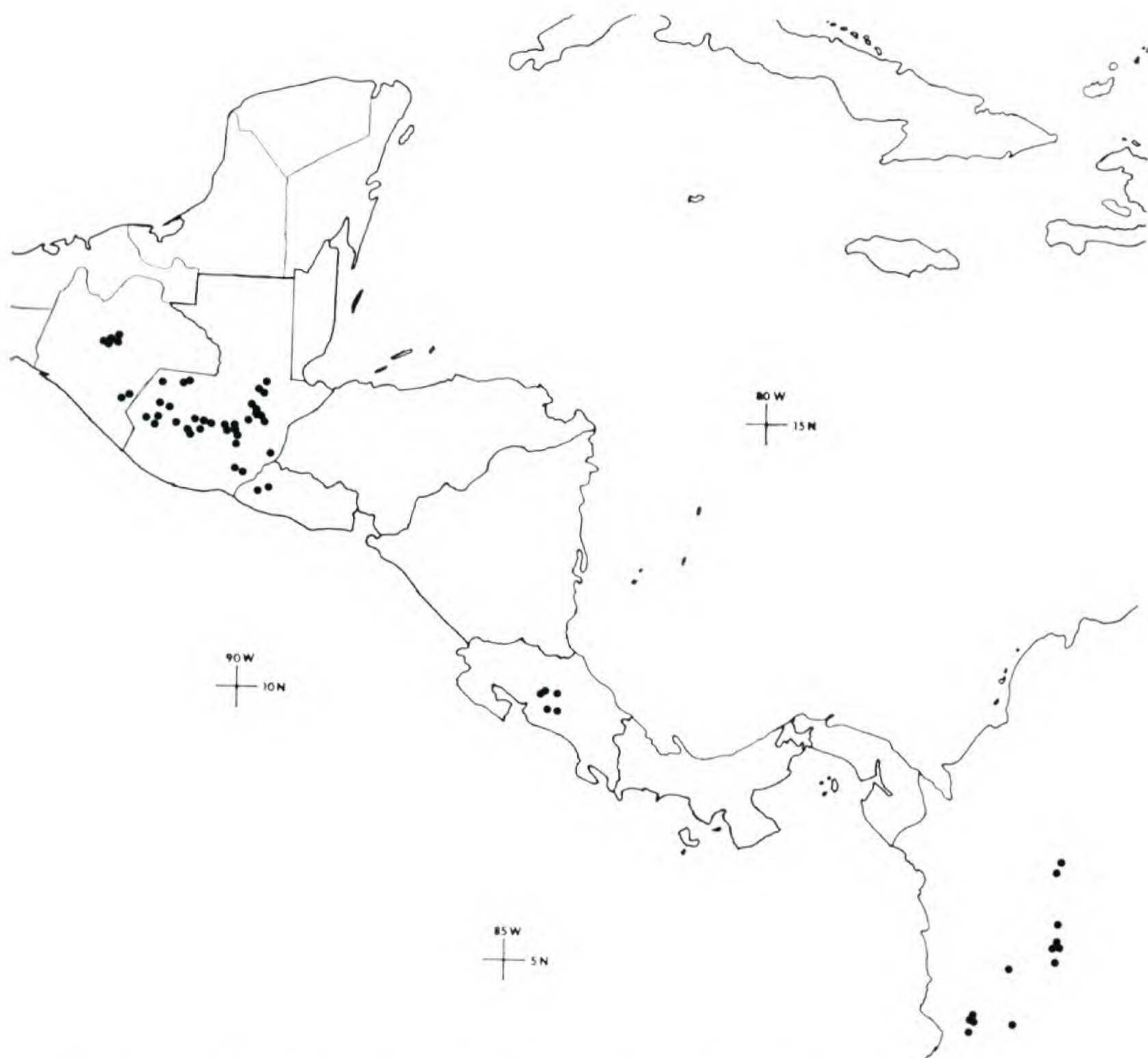
Dahlia lehmannii var. *leucantha* Sherff, *Am. Jour. Bot.* 38: 70. 1951. Type: *Austin Smith* A-620, San Luis de Zarcero, Costa Rica (F!).

Herbaceous or suffrutescent perennial, 2-6(-9) m. tall. Stems of the previous year becoming woody, 7-10 cm. diam.; stems of the current year essentially unbranched except in the flowering portion, 1-4 cm. diam., hollow but septate at the nodes, smooth, obscurely 6-angled, glaucous, green or reddish-green when fresh, when dry becoming minutely many-striate with conspicuous lenticels, surface of older portions rough and tan or brown with enlarged lenticels. Leaves 50-90 cm. long, 2- or 3-pinnate; primary leaflets 11-15, basal pinnae of principal leaves 20-38 cm. long; simple basal pinnules of lowest pinnae 5.5-14 cm. long, 3.5-6 cm. wide, ovate to oblong elliptical, acuminate or rarely merely acute at tips, mostly tapered or rounded at base, sometimes truncate or subcordate, sessile or stalked, the stalks rarely exceeding 5 mm.; the upper surface green, with hairs of two kinds, those on the nerves minute and appressed, those between the nerves longer, erect or slightly bent, the lower surface lighter green

or gray-green, reticulate veiny, with hairs long, flexuous, conspicuously multi-cellular, mostly following the nerves; margins obscurely or conspicuously ciliolate, regularly and more or less evenly serrate with (6-)10-18 teeth per side; stipels occurring irregularly, when present then usually at the fourth rachis node but sometimes at more proximal nodes as well, infrequently also at the first node on the basal rachilla; petiole 12-25 cm. long, adaxially flattened or longitudinally grooved, abaxially rounded, glabrous, solid or sometimes hollow, strongly dilated and fleshy at the base, connate with the petiole base of the opposite leaf to form a conspicuous cupule at the node; rachis glabrous except for a cluster of hairs at the junctions with the primary pinnae, adaxially grooved, becoming narrowly winged esp. in the distal portions. Heads numerous, sometimes 150-300 per plant, obliquely erect to slightly nodding (pendulous in some horticultural clones), 9-15 cm. diam., slightly campanulate at anthesis; outer involucral bracts reflexed at anthesis, 6-14 mm. long, 3-9 mm. wide, obovate or oblanceolate, obtuse or acute, rarely subacuminate, dorsally many-striate, glabrous, ventrally appressed pubescent, the hairs stramineous or brown; inner bracts 15-25 mm. long, 7-13 mm. wide, ovate, obtuse, many-lined, brown with hyaline margins; rays white or whitish-lavender to rose-purple, 3.5-6 cm. long, 1.5-3 cm. wide, elliptical or ovate, acute or subacute, denticulate, tube of the ligulate florets pubescent, the hairs sometimes gland-tipped; disc florets 128-172, yellow or yellow with reddish tips, 9-11 mm. long, corolla lobes reflexed and inwardly curled; style branches about 3 mm. long, less than 1 mm. wide, lanceolate-attenuate, sometimes abruptly rhomboid-broadened near the middle; chaff (in fruit) about 2 cm. long, brown, sometimes with reddish or purple tips; achenes 13-17 mm. long, 1.8-2.5 mm. wide, linear or slightly oblanceolate. Chromosome number, $n = 16$.

Rocky slopes and fields, 2500-9000 ft., central Chiapas southeast in Guatemala, San Salvador, Costa Rica, and Colombia. Flowering Sept.-Feb. Map 1.

MEXICO. CHIAPAS: from 3 to 10 mi. E. of San Cristóbal de las Casas along route 190, *Breedlove* 7300 (DS, F, MICH), *Carlson* 1613 (F), *Melchert et al.* 6462 (IA), 6464 (IA), *Miranda* 9188 (MEXU), *Moore & Cetto* 8189 (BH, MEXU), *Nelson* 3173 (GH, US [2]); vicinity of Tenejapa, *Breedlove* 6814 (DS, F), 7233 (DS, F[2]); 5 mi. S. of Jitotól, *Breedlove* 8878 (DS, F); Cerro Ovando, *Matuda* 2233 (GH, MEXU, MICH, US); Cerro Male, *Matuda* 4628 (MO, NY); near Motozintla, *Matuda* 15452 (MEXU). COSTA RICA. without specific locality, *Stork* 2992 (F). ALAJUELA: San Luis de Zarcero, *Austin Smith* A620 (F, MO), H236 (F, MO), NY1369 (F, GH, NY). SAN JOSE: Las Nubes, Coronado, *Echevarria* 160 (F, UC), *Stork* 4722 (GH, MICH, NY, UC); Santa María de Dota, *Standley* 41857 (GH, US). EL SAL-



Map 1. Distribution of *Dahlia imperialis* Roezl ex Ortgies.

VADOR. AHUACHAPAN: Apaneca, *Calderon* 2422 (F, US). SANTA ANA: Volcán de Santa Ana, *Tucker* 1297 (UC). GUATEMALA. ALTA VERAPAZ: vicinity of Cobán, *Standley* 69469 (F), 90887 (F), 91114 (F); Socoyocté, *Maxon & Hay* 3295 (Type of *D. maxonii*—US); above Santa Cruz, *Standley* 71026 (F). CHIMALTENANGO: Chichavác, *Skutch* 65 (US), 711 (GH); above Las Calderas, *Standley* 80260 (F). CHIQUIMULA: vicinity of El Barriol, *Steyermark* 30774 (F). GUATEMALA: NE. of Guatemala City, *White* 5142 (MICH). HUEHUETENANGO: vicinity of San Mateo Ixtatán, *Steyermark* 49887 (F); *Breedlove* 8761 (DS, F); above Concepción, *Goodman & Melhus* 3691 (F, ISC); near Huehuetenango, *Melchert et al.* 6452 (IA); vicinity of Tunima, *Steyermark* 48418 (F). JALAPA: vicinity of Jalapa, *Steyermark* 32110 (F), 32406 (F), 32547 (F), *Standley* 77180 (F), 77228 (F). JUTIAPA: Volcán Suchitán, *Steyermark* 31903 (F). QUETZALTENANGO: vicinity of Santa María de Jesús, *Standley* 67162 (F); 84874 (F); slopes of Volcán Santa María, *Steyermark* 34414 (F), 34415 (F); slopes of

Volcán Zunil, *Standley* 67468 (F), *Steyermark* 34676 (F); SE. of San Martin Chile Verde, *Standley* 83790 (F), SE. of Palestrina, *Standley* 84205 (F); along route 1, E. Quetzaltenango, *Melchert et al.* 6434 (IA). SACATEPEQUEZ: slopes of Volcán de Agua, *Bell & Duke* 16972 (MICH, UC), *Hunnewell* 14869 (GH), *Standley* 59425 (F); near Antigua, *Kellerman* 7096 (F, MICH, NY, US); San Rafael, *J. D. Smith* 2857 (F, US); above Las Calderas, *Standley* 59972 (F) barranca above Duenas, *Standley* 63214 (F). SAN MARCOS: along road between San Marcos and San Rafael Pié de la Cuesta, *Standley* 85320 (F), 86289 (F, GH); Cenaguilla, *Heyde & Lux* 4239 (F, GH, MO, NY, US). SOLOLA: E. of Sololá along road above Lake Atitlán, *Melchert et al.* 6439 (IA), 6443 (IA). TOTONICAPAN: 5 mi. E. of Quetzaltenango, *Melchert et al.* 6434 (IA). COLOMBIA. CALDIAS: Río Quindío, above Armenia, *Pennell et al.* 8677 (GH, NY, US). CAUCA: Vicinity of Popayán, *Cuatrecasas* 23407 (F), *Fosberg* 20290 (NY, US), *Killip & Lehmann V* 38056 (GH, UC, US), *Lehmann* 4894 (Holotype of *D. lehmannii* — B [?], Isotype — F); *Sneidern* 5677 (US); El Tambo, *Sneidern* 1035 (F, GH, NY). CUNDINAMARCA: vicinity of Bogotá, *Ping* 157 (F, MO), *Soejarto* 281 (GH); between El Salto and El Colegio, *Cuatrecasas* 8185 (F, US); Taguate Valley, *Grant* 9652 (US); Subatá, *Haught* 6114 (US); near Charquito, *Langenheim* 3359 (UC); barranca del Río Bogotá, *Schultes et al.* 4045 (US). HUILA: Río Balsallas, *Rusby & Pennell* 929 (GH, NY, US). SANTANDER: E. slope of Paramo del Hatico, *Killip & A. C. Smith* 20558 (A, GH, NY, US); valley above Suratá, *Killip & A. C. Smith* 16530 (GH, NY, US). The following specimens from cultivation: GUATEMALA. SACATEPEQUEZ: near Antigua, *Sherff* 5054 I, II, III, IV, V (F). MEXICO. DISTRITO FEDERAL: *Martinez s.n.* (MEXU), in Cetto Garden, Jardines Pedregal near Tizapán, *Moore s.n.* (BH). UNITED STATES. CALIFORNIA: Golden Gate Park, San Francisco, *Walther s.n.* (CAS). IOWA: University of Iowa Experimental Gardens, Iowa City, *Sorensen* 6249 (IA).

After having observed the so-called "tree-dahlias" in their native environment as well as having grown living plants in the gardens and the greenhouses at the University of Iowa, I can find no sound biological basis for maintaining the several taxa into which they have been segregated previously.

Dahlia lehmannii var. *leucantha* was established on the basis of its whitish rather than lavender ligules and its geographic restriction to parts of Costa Rica. Reports from the field (Burger, personal communication, observations of Standley, 1938, and specimen label of *Stork* 4722 [GH, MICH,

NY, UC]) indicate that ligule color in wild populations ranges from white to lavender or light purple. This suggests that genetic control of ligule color is most likely multi-factorial, the color-range due to random segregation of quantitative and/or qualitative factors. This same color range has also been observed in populations of *D. merckii*, *dissecta*, and *scapigera*.

Sherff's (1951 & 1955) recognition of *Dahlia lehmannii* as a separate species from *D. imperialis* stems from the fact that plants on which he based the latter name were from an unusual and widely cultivated horticultural clone.² Individuals of this particular clone are, according to Sherff (1955), characterized by excessively drooping heads and smaller ultimate leaf segments (4-7 cm. not 5.5-14 cm. long). I was able to obtain cuttings from what I believe is the same clone mentioned by Sherff (footnote 10, 1951a). During the summer of 1966 these plants were grown alongside wild plants raised from seeds collected in the mountains of Chiapas (*Breedlove* 7424, voucher at DS). By mid-October all of the plants had attained a height of about 5.5 ft. and bore fully developed leaves. At this stage individuals of the two groups were, on the basis of their total morphologic appearance, essentially indistinguishable from each other. Only detailed comparison of them revealed minor differences. For example, the unfolding leaves of the Chiapas plants produced a slight reddish pigmentation which was not seen in the cloned individuals. It was also observed that their mature leaflets were apically more acuminate and less pubescent on the upper surface. Unfortunately these plants were cut down by frost before reaching the flowering stage.

A plant from the cultivated clone which had been planted in the earthen floor (not in a pot) of the "tree-house" at the University of Iowa grew to maturity and flowered. Its heads were seen to be no more pendulous than those on

²Its clonal nature is suggested by the information (Turlington, personal communication,) that "*D. imperialis* has never set seed; it has always been propagated by cuttings or root division."

plants observed in wild populations in Chiapas and Guatemala. As each head on this plant neared the end of anthesis, an apparent abscission layer formed on the peduncle just beneath the head causing the heads to fall. This "flower-drop" is perhaps the result of the heads not having been suitably pollinated considering that this plant is reproductively self-incompatible. Such an hypothesis is, as yet, untested.

Sherff noted that *Dahlia imperialis* (i.e., the cultivated clone) bore leaflets much smaller than the wild "tree-dahlias" (i.e., *D. lehmannii*). I have observed that when these plants are grown in pots in the greenhouse their leaves tend to be smaller than when field grown or when grown in the earthen floor of a tree-house. It is quite likely that Sherff used a greenhouse-grown specimen for his description. He writes (1951b) of having "raised noble specimens of this species [i.e., *D. imperialis* sensu Sherff (1955)] for several years in the greenhouses of the University of Chicago . . . and of the Chicago Teachers College."

In my judgment the cultivated form of *Dahlia imperialis* does not differ sufficiently from the wild plants to warrant treating it as a distinct species. The minor differences displayed in the cultivated individuals, as compared to those collected in the field, are of no greater magnitude than one finds from plant to plant within a reasonably large wild population in its native environment.

Dahlia imperialis may be distinguished from the other "tree-dahlias" by its 9-15 (not 3-7) primary leaflets. It should perhaps be emphasized that median leaves, or at least a portion of them, are essential in determinations of these species.

3. ***Dahlia tenuicaulis*** Sorensen sp. nov. TYPE: MEXICO: OAXACA: 13 mi. NE. of village of Ixtlán de Juárez along route 175, Oaxaca-Tuxtepec, in cloud forest, about 9000 ft., 25 Aug. 1965, *Melchert & Sorensen* 6194A (Holotype: IA!, 125,512 & 125,513).

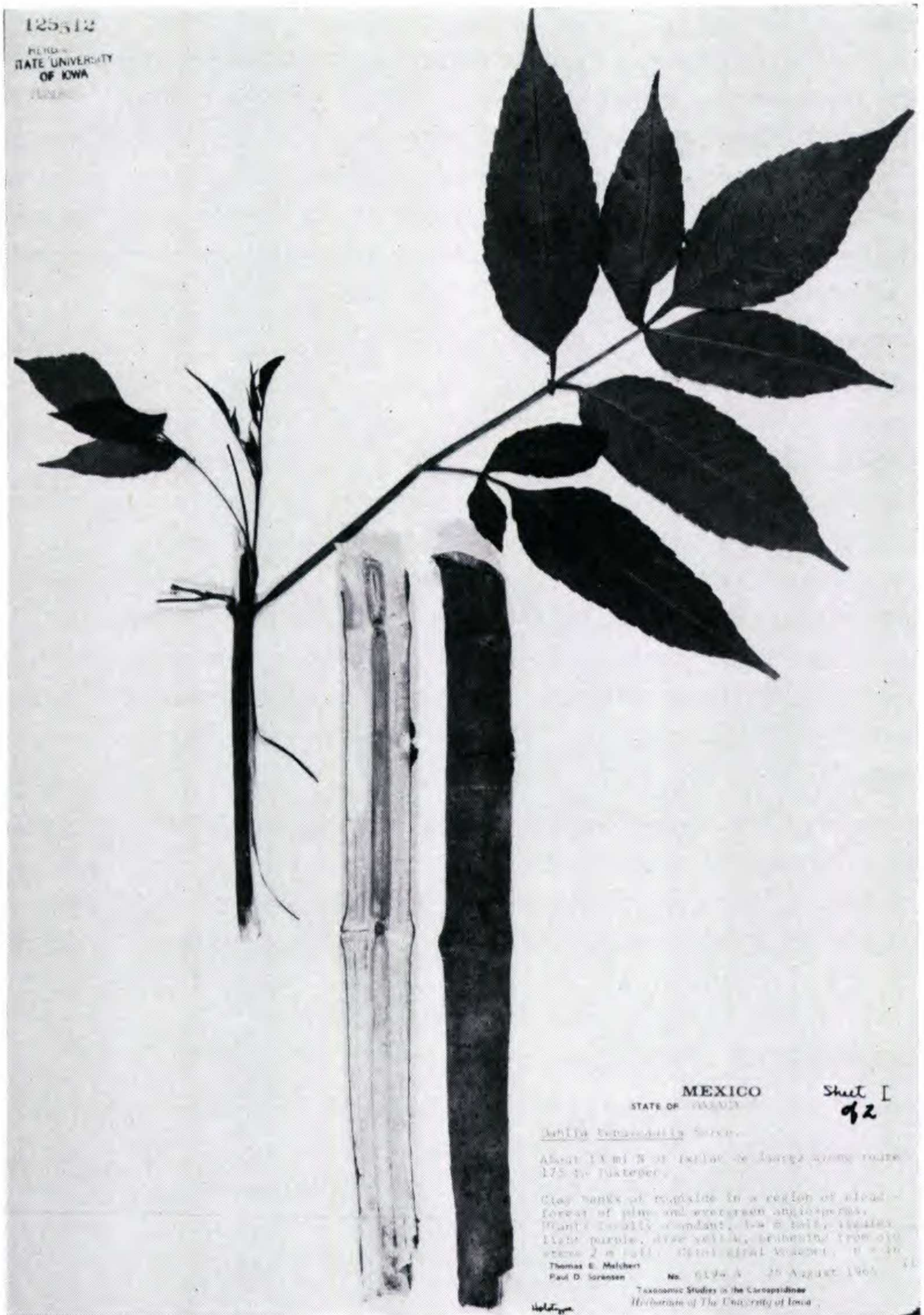
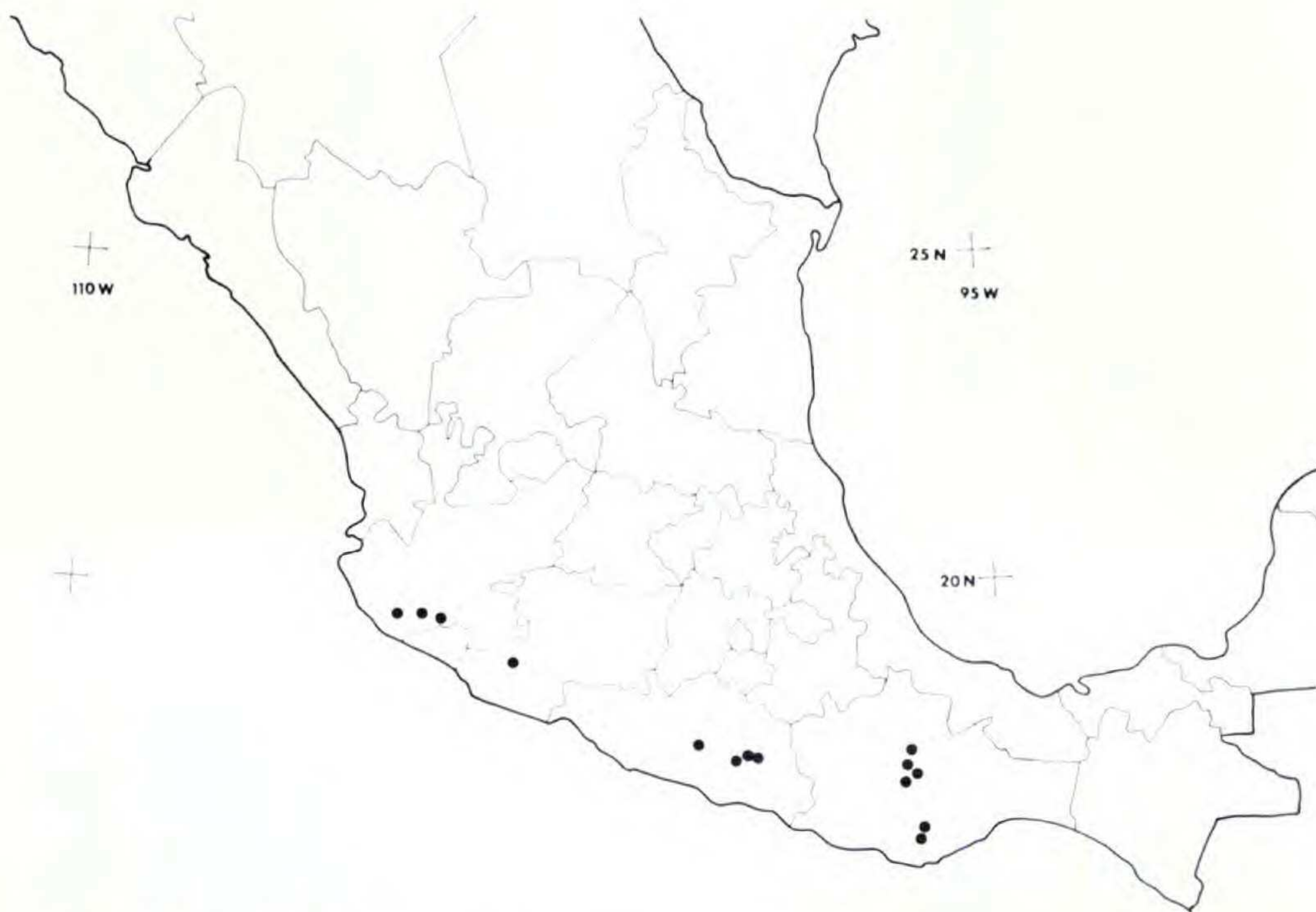


Fig. 2. *Dahlia tenuicaulis* Sorensen. Photograph of type (IA),
× 1/3.

Suffrutex, 21-37 dm. altus. Caules lignosi anni praecedentis 1.5-3 cm. diametro. Folia pinnata vel bipinnata, 27-43 cm. longa; foliolis 3-7, pinnis basilaribus 10-18 cm. longis et petiolulis 2-4 cm. longis, marginibus regulatim serratis cum dentibus in quoque latere 8-14. Capitula 12 vel plura in quoque ramo principali, squammis exterioribus involucri reflexis sub anthesi, 8-12 mm. longis, 2-4 mm. latis. Flores ligulati lilacini, 2.8-4 cm. longi, 1-2 cm. lati; flores tubulosi 70-80. Achenia lineari-oblongata, 11-15 mm. longa, 1-2 mm. lata. Chromosomatum numerus: $n = 16$. Fig. 2.

Cool cloud forests of *Pinus*, *Abies* and *Arbutus*, deep loamy soil, 8500-10,000 ft., from the type locality in Oaxaca westward on tall peaks to near Santa Monica (about 104° 30' w. long, 19° 15' n. lat.), Jalisco. Flowering Aug.-Oct. Map 2.



Map 2. Distribution of *Dahlia tenuicaulis* Sorensen.

MEXICO. MICHOACAN: Cerro Torricillas, *Hinton* 12364 (GH, MICH, NY, US). JALISCO: slopes of Nevado de Colima, *McVaugh* 11745 (MICH), 12926 (MICH), *Melchert et al.* 6396 A-C (IA); Cerro de Manantlán, 15-20 mi. SE. of Autlán, *McVaugh* 13873 (MICH); near Santa Monica, *McVaugh* 14110 (MICH). OAXACA: slopes of Cerro San Felipe, *Conzatti & Gonzalez* 552 (GH, MEXU, US), *Conzatti* 2259 (F), *Pringle* 5875 (GH), *C. L. Smith* 295 (F, IA, MO, NY, US);

from 10 to 13 mi. NE. of Ixtlán de Juárez, *Melchert & Sorensen* 6193 (IA); 9 mi. above La Soledad along road to Oaxaca, *Moore* 8247 (BH, MEXU); near K-152 below Suchixtepec, *Moore* 8250 (BH, MEXU); 18 mi. SW. of Oaxaca, *Nelson* 1355 (US); Cerro de Pluma, vicinity of Suchixtepec, *Reko* 3716 (US). GUERRERO: vicinity of Cerro Teotepec, *Hinton* 11083 (GH), 11137 (GH, MICH), *Rzedowski & McVaugh* 163 (MICH); 40 k. W. of Chilpancingo, *Feddema* 2746 (MICH); summit of Sierra Madre near Chilpancingo, *Nelson* 2193 (US); river gorge near Omiltemi, *Sharp* 441534 (F).

Among the "tree-dahlias" *Dahlia tenuicaulis* is the only species endemic in México. It is most easily distinguished from *D. excelsa* and *D. imperialis* by the overall smaller size of its leaves (27-43 cm. not 50-90 cm. long). From *D. imperialis* it is further distinguished by its 1- or 2-pinnate (not 3-pinnate) leaves, by its fewer number of disc florets (70-80 not 120-170) and by its rather slender ligneous stems which barely exceed 2.5 cm. diam. (not 4-10 cm. diam.). There is complete overlap between the species in the size and long-attenuate apices of their leaflets or ultimate segments. In the field it was observed that some individuals of *D. imperialis* produced their current season's growth directly from tuberous roots not exclusively from the previous year's stems as does *D. tenuicaulis*. Unlike *D. imperialis*, which is usually found in open disturbed areas along roadsides and in fields, *D. tenuicaulis* appears to be restricted to dense *Pinus*, *Abies* and *Arbutus* cloud forests at elevations of 8,500 to 10,000 ft.

Section 2. Epiphytum Sherff, Bot. Leaflet 4: 21. 1951.

Type species: *Dahlia macdougallii* Sherff.

Plants epiphytic on tall trees, the stems elongate, solid, ligneous, the roots elongate, aërial, reaching down into the earth. (Species 4.)

4. ***Dahlia macdougallii*** Sherff, Bot. Leaflet 2: 5. 1950, & Chicago Nat. Hist. Mus. Bull. 22(6): 5-7, *illus.* 1951. TYPE: MEXICO: OAXACA: about 50 mi. W. of Tehuantepec, 7000-7500 ft., in rain forest above town of Santo Tomás Teipán, Nov. 1949, *MacDougall s.n.* (Holotype: F, sheet number 1,449,390; Isotype: F!).

Perennial, epiphytic on tall trees. Stems solid and woody, about 5 cm. diam., reaching about 10 m. to the tree tops where the flowering branches sprawl for considerable distances. Aërial roots about 5 cm. thick, up to 22 m. long. Uppermost leaves (median or principal leaves not seen) pinnate, 18-27 cm. long; leaflets 3-5, basal pinnae 13-15 cm. long, 4-5 cm. wide, ovate or elliptic-ovate, long-acuminate, the base of principal pinnae at least broadly rounded or almost cordate, sometimes asymmetric bearing a sessile lobe on the proximal side at the base of the main blade; surfaces bicolored, dark green above, gray-green and conspicuously veiny beneath, the upper pubescent along the principal veins and near margins, the lower almost glabrous but with a cluster of brown hairs at the junctions of the main veins; margins ciliolate, the cilia soft and flexuous, antrorsely curved, sharply and regularly serrate-dentate with 15-23 teeth per side; petiole 4.5-10 cm. long, flattened above and rounded below, semi-circular in cross-section, essentially glabrous; rachis glabrous; stipels present at median rachis nodes and sometimes at the base of the terminal leaflet when the latter is not decurrent-winged. Heads numerous, at least as many as 14 per main flowering branch, erect or obliquely erect; outer involucral bracts spreading or reflexed at anthesis, 10-14 mm. long, 2-3 mm. wide, lanceolate or rarely oblanceolate, acute or acuminate, dorsally many-lined, glabrous, ventrally appressed pubescent; inner bracts 12-15 mm. long, 3-6 mm. wide; rays white or at least whitish, 4.2-5 cm. long, 1.2-2.2 cm. wide, elliptical or oblong lanceolate, mostly acute at the apex; disc florets yellow; achenes not seen.

I have seen specimens from the type locality only, but Sherff (1951b) states that Thomas MacDougall has observed the species on Cerro Chivato in the territory of the village of San José Quianite which is in the same general area as the type locality. Flowering Nov.

MEXICO. OAXACA: above town of Santo Tomás Teipán, *MacDougall* 21984 (Topotype: NY).

Though not as large, the leaves of *Dahlia macdougallii* bear a strong resemblance to those of the "tree-dahlias." The manner of arrangement of the heads in corymbose clusters at the end of flowering branches is also a feature this species shares with *D. imperialis* and *D. tenuicaulis*. Its unique habit, however, distinguishes it from all other known species.

Sherff (1962) states that some European scientists have been at work on the cytology of *D. macdougallii* but in a

personal communication with him and with the directors of the botanic gardens at Stockholm and Göteborg, Sweden, there is no indication that this work has ever been carried forward.

Section 3. **Entemophyllon** Sorensen, sect. nov. Type species: *Dahlia dissecta* S. Wats.

Herba perennis vel suffrutex, 6-15 dm. alta. Caules numerosis e radicibus tuberosis, plus minusve perennis, lignescentes, 4-20 mm. diametro, caules novi 1.5-12 mm. diametro, saepe cum medulla dissepimentis vel cum dissepimentis incompletis. Folia subtiliter dissecta, pinnati-pinnatisecta vel tripinnati-pinnatisecta cum foliolis oppositis et pinnulis alternis. Squammae exteriores involucri erectae vel ascendentes sub anthesi. Flores ligulati albi, albido-lavanduli vel lilacini, inferne saepe cum macula lutea vel luteo-viridi. Achenia minute tuberculata. Chromosomatum numerus: $n = 17$. (Species 5-9) (see Map 3).

Species 5-9 which comprise the new section *Entemophyllon* form a coherent evolutionary series within the genus *Dahlia*. Members of this section share a number of characteristics either rare or absent among the other species of the genus.

Cytological information has been gathered for three of the five taxa of this section: *Dahlia dissecta* var. *dissecta*, *D. foeniculifolia*, and the new *D. rupicola*. All have a meiotic chromosome number of $n = 17$, a number not reported previously for the genus (cf. footnote 1). Pairing appears to be completely regular, forming 17 perfect bivalents at diakinesis.

In habit of growth all of the species produce many stems arising from a common tuberously thickened rootstock. This is in marked contrast to the usual single-stemmed (or in section *Pseudodendron*, 3-4-stemmed) habit of all other species of the genus. The stems of several species in section *Entemophyllon* live for more than one season becoming quite woody and giving full grown plants a shrubby aspect. Their wood, however, remains rather weak and brittle and the stems rarely exceed 1.5 cm. diam. Pith in the stems of the current season's growth (of all taxa except *D. foeniculifolia* and *D. dissecta* var. *dissecta*) is solid in the early stages

becoming chambered in age or sometimes the diaphragms (about 3 mm. apart) themselves disintegrate leaving behind annular rudiments on the wall of the pith cavity. When crushed or bruised, the herbage of these species emits a particularly strong carrot odor. The segmentation of their leaves is probably the most remarkable characteristic of these species. They all are rather highly dissected (somewhat less so in *D. scapigeroides*) and are at least pinnate-pinnatisect or more often bipinnate to bipinnate-pinnatisect. The primary leaflets are arranged oppositely on the rachis, but the pinnules of the secondary and lesser ranks are arranged alternately on their rachillae. This characteristic is found with the same consistency in just one other species, *D. merckii*.

A rather interesting occurrence attending the circumscription of section Entemophyllon took place while I was preparing for a chromatographic analysis of the secondary biochemical compounds in the leaves of these species. As a first step in this technique, dried leaves were crushed and placed in a flask with acidified methyl alcohol (0.5% or 1% conc. HCl, V:V). After about 12 hours on an orbital shaker the liquid turned milky-green. Upon filtration it was seen that the milky color had been caused by the formation of a water-white, crystalline compound. This precipitate apparently is limited within the genus to the six taxa of section Entemophyllon. The precise nature of the compound remains to be determined, but efforts toward its elucidation are presently in progress.

5. **Dahlia scapigeroides** Sherff, Am. Jour. Bot. 34: 145. 1947. TYPE: MEXICO: HIDALGO: near Ixmiquilpan, Aug. 1905, *Rose, Painter & Rose* 9157 (Holotype: GH!; photo. F!; Isotype: US!).

Dahlia scapigeroides var. *typica* Sherff, Am. Jour. Bot. 34: 145. 1947. Type: as for *Dahlia scapigeroides* Sherff.

Suffruticose perennial reaching 24.5 dm. tall. Stems of the previous season 6-8 mm. diam.; pith chambered or the diaphragms incomplete with only annular rudiments of the septa on the inside wall of the

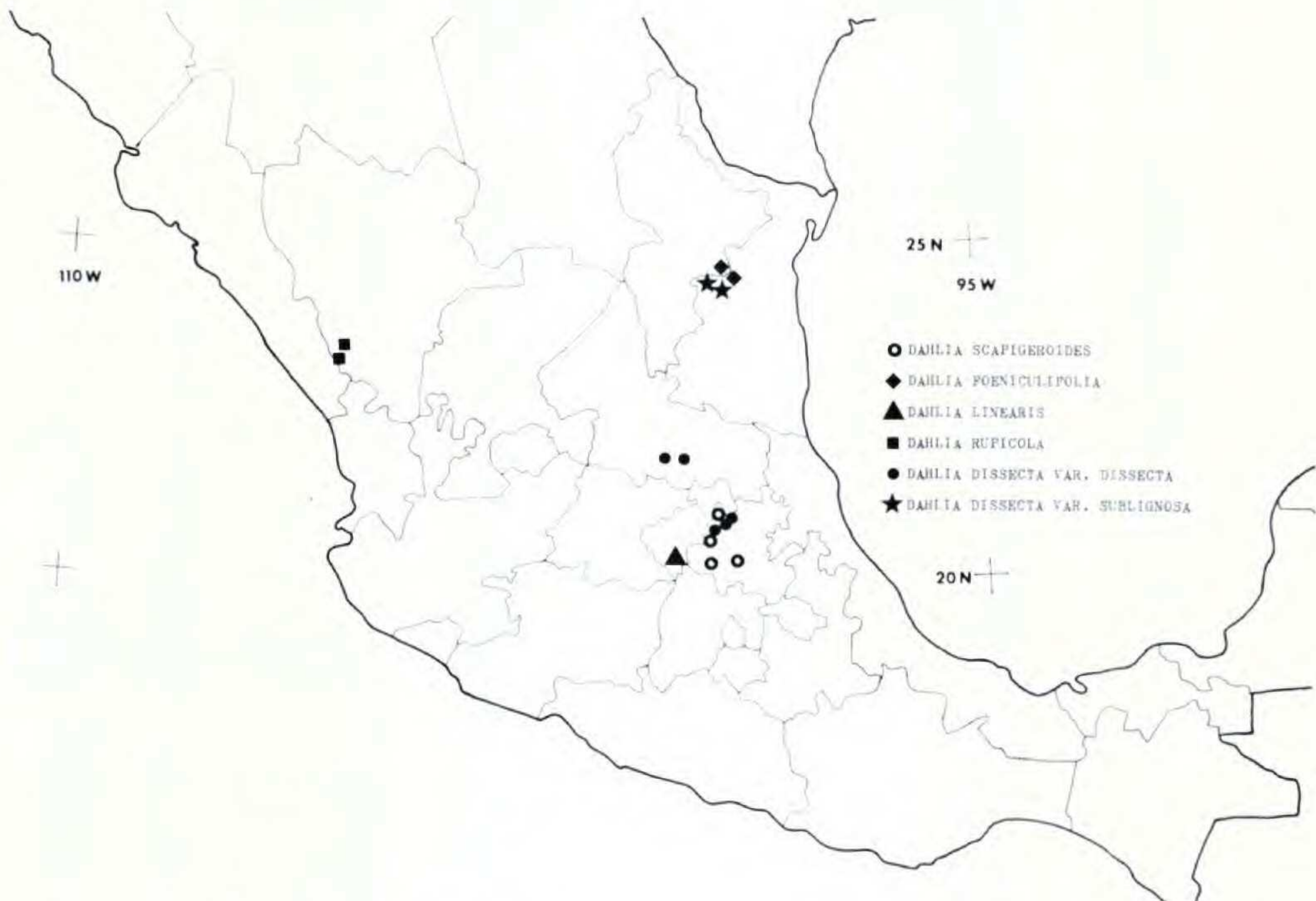
pith cavity; exterior surface glabrous, pruinose, longitudinally striate, the conspicuous lenticels orbicular or vertically elongate; stems of the current year 5-7 mm. diam., longitudinally striate, glabrous, pruinose; internodes 2-3 cm. long. Leaves pinnate-pinnatisect to bipinnate, 10-16 cm. long, leaflets 5-7, opposite on the rachis, basal pinnae 5-9.5 cm. long, sessile or stalked, petiolules 2-11 mm. long, ultimate segments alternate on the rachilla, 1-2.5 cm. long, 5-16 mm. wide, ovate-lanceolate, acute; surfaces more or less glabrous, occasionally with a few very fine scattered hairs below; margins eciliolate, irregularly and coarsely serrate, 1-4 teeth per side; stipels 0.6-4.5 cm. long, 2-15 mm. wide, ovate, acute, occurring irregularly, when present then only at the junctions of the petiolulate pinnae; petiole 5-7 cm. long, crescent-shaped in cross-section, grooved above; rachis grooved above, glabrous except for a cluster of hairs at the junctions with the pinnae. Heads obliquely erect at anthesis, 1-2 per branch on peduncles 9-14 cm. long; outer involucral bracts erect at anthesis, 14-17 mm. long, 5-11 mm. wide, broadly ovate, obtuse, 4-8-lined, the nerves blackish, sometimes faintly reticulate veiny, ventrally puberulent, dorsally glabrous; inner bracts 15-18 mm. long, 6-10 mm. wide; chaff (in fruit) 18-20 mm. long, 5-8 mm. wide; rays lavender or rose-purple, 2.5-4 cm. long, 14-18 mm. wide, ovate, acute or denticulate; disc florets yellow; style branches 2.8-3 mm. long, less than 0.5 mm. wide; achenes 12-15 mm. long, 1.7-2 mm. wide, linear, slightly wider above the middle, longitudinally sulcate, surfaces beset with numerous minute tuberculae; pappus absent or consisting of 2 minute, squarrose rudiments usually less than 1 mm. long.

In dry, rocky places among thorny scrub, 4700-6500 ft., western Hidalgo. Flowering June-Sep. Map 3, open circles.

MEXICO. HIDALGO: cañons, vicinity of Ixmiquilpan, *Purpus* 1341 (F, MO, NY, UC), 5577 (UC); Barranca Grande de Metztitlán, *Moore* 3097 (BH, GH); barranca between Jacala and Tepetates, *Moore* 5036 (BH); near highway SE. of Jacala, *Moore & Wood* 3932 (BH, GH, NY, UC); along road from Zimapán to Mina Loma del Toro, *Moore & Wood* 4407 (BH, GH).

When Sherff (1947) established *Dahlia scapigeroides* and its variety *apiculata* (i.e., *D. apiculata*) he referred to their similarity in growth habit with *D. scapigera*. He noted especially the shortened internodes with leaves crowded near the base of the stem. *D. scapigera*, however, is herbaceous (not suffrutescent) and its current year's growth is from underground tubers, not from ligneous stems of the previous year as in *D. scapigeroides*.

In addition to its woody stems, several other character-



Map 3. Distribution of the species comprising Section 3, Entemophyllon: *Dahlia scapigeroides* Sherff, open circles; *Dahlia foeniculifolia* Sherff, solid diamonds; *Dahlia linearis* Sherff, solid triangle; *Dahlia rupicola* Sorensen, solid squares; *Dahlia dissecta* var. *dissecta*, closed circles; *Dahlia dissecta* var. *sublignosa* Sorensen, stars.

istics of *D. scapigeroides* (e.g. chambered pith, alternate pinnules, a crystalline precipitate in an acidified methanolic extract of its leaves) clearly place it in the section Entemophyllon. It may be distinguished from other members of this section on the following characteristics: from *D. dissecta* vars. and *D. linearis* on the size of its outer involucre bracts (5-11 mm. not 1.8-5 mm. wide); and from *D. foeniculifolia* and *D. rupicola* on the width of its ultimate segments (5-16 mm. not 0.5-2 mm. wide).

6. ***Dahlia foeniculifolia* Sherff, Am. Jour. Bot. 38: 70. 1951.**

TYPE: MEXICO: NUEVO LEÓN: Dulces, Nombres, open rocky slope, 2000 m., 8 Aug. 1948, *Meyer & Rogers* 2881 (Holotype: US!; Isotypes: F!, GH!, MICH!, MO!, US!).

Herbaceous perennial, producing several canes 14-19 cm. tall from a tuberously thickened rootstock. Stems 5-12 mm. diam., glabrous

except for a cluster of hairs at the nodes, light reddish-brown or purple; internodes 8.5-13.5 cm. long, many-striate. Leaves bipinnate-pinnatisect, 8-33 cm. long (including petiole)³; primary leaflets 7-17, the basal pinnae 15-19 cm. long, their pinnules alternate on the rachilla, the ultimate segments narrowly linear 0.5-2 mm. wide, tips long-attenuate, one-nerved, pubescent in the young foliage, mature leaves minutely pubescent or glabrate, green on both sides; margins smooth; petiole from less than 0.5 cm. to 3.5 cm. long; rachis essentially glabrous except for a cluster of hairs at the junction with the pinnae. Heads few, 1-4 per stem, obliquely erect, elevated on peduncles 8-15 cm. long; outer involucral bracts erect at anthesis, ovate to oblong-ovate, 14-18 mm. long, 8-11 mm. wide, conspicuously several to many-purple-lined, the lines running almost to the obtuse or acute tips, dorsally sparingly pubescent or glabrous, ventrally puberulent; inner bracts 15-18 mm. long, 6-9 mm. wide; rays lavender or light reddish-purple, 3.5-6 cm. long, 1.6-2.1 cm. wide, oblong-ovate, acute or denticulate; disc florets yellow, the anthers yellow and long exserted; achenes not seen.

Rocky slopes and ledges, about 6500 ft., Nuevo León and Tamaulipas. Flowering June-Aug. Map 3, solid diamonds.

MEXICO. TAMAULIPAS: 3-5 km. S. of Huitsachél, 6000 ft., *Stanford et al.* 2130 (F, NY, TEX, US).

Dahlia foeniculifolia shares with *D. dissecta* var. *dissecta* its herbaceous habit and the absence of chambered pith. The two are easily distinguished on the dimensions of their outer involucral bracts (14-18 mm. long in the former, 5-7 mm. long in the latter, including also var. *sublignosa*). The outer bracts of *D. foeniculifolia* compare in size to those of *D. scapigeroides* from which it is separated by the much narrower ultimate segments of its leaves (0.5-2 mm. not 5-16 mm. wide) and its herbaceous habit. The highly dissected leaves with very narrow ultimate segments of *D. foeniculifolia* resemble strongly those of the allied *D. rupicola* and *D. linearis*. These species, though apparently both quite closely related to *D. foeniculifolia*, have a suffrutescent growth habit.

7. ***Dahlia linearis*** Sherff, Bot. Gaz. 89: 364. 1930. TYPE: MEXICO: QUERÉTARO: Querétaro (the exact locality

³Only one specimen (*Meyer & Rogers* 2881 at F) has complete median leaves measuring 29-33 cm.; other specimens I have examined possess only leaves from the flowering portion of the stems, these measure 8-15 cm. long.

not given), 1850 m., 1910-1913, *Agniel* 10286 (Holotype: MO!, photo. F!; Isotype: US!).

Suffruticose perennial 8-13 dm. tall, freely branching from tuberously-thickened roots and ligneous stems of the year before. Stems of the previous year 4-8 mm. diam., longitudinally striate, some parts covered with a scaly gray bloom; lenticels conspicuous, vertically oblong, the larger ones 1-2 mm. long; pith chambered; stems of the current year 1.5-5 mm. diam., glabrous, many sulcate, markedly pruinose esp. in the middle portions, the pith solid in younger parts, in older parts becoming chambered; median internodes 3.5-11 cm. long. Principal leaves pinnate-pinnatisect to bipinnate-pinnatisect, 12-18 cm. long; primary leaflets 7-9, their pinnules alternate on the rachilla, the basal pinnae 3.5-9 cm. long; ultimate segments 0.9-2.3 cm. long, their lobes 1-5.5 mm. wide, linear-lanceolate, one-nerved, tips long attenuate-mucronate; surfaces glabrous or with a line of fine hairs along the veins above; stipels usually present on median leaves, attached at the basal and second rachis nodes, 1-5 cm. long; margins smooth; petiole 4-6.7 cm. long, glabrous or with two lines of fine hairs above in the proximal portion; rachis grooved above, minutely hispidulous or glabrous but usually with a cluster of hairs at the junction with the pinnae. Heads obliquely erect at anthesis, usually 2-6 on a stem, on peduncles 1.5-10 cm. long; outer involucre bracts 5-9 mm. long, 2-3.5 mm. wide, oblong-lanceolate, tips acute or subacuminate, dorsally glabrous, green, 4-7 purple-lined, ventrally sparsely pubescent; inner bracts 11-15 mm. long, 4-8 mm. wide, usually glabrous but sometimes with fine hairs near the base; chaff (in fruit) 10-12.5 mm. long, 4-6 mm. wide, stramineous with a smudge of yellow near tip; rays purple with a yellow spot at base, 1-2.1 cm. long, 0.9-1.3 cm. wide, ovate, acute or denticulate; disc florets 43-48, yellow, anthers conspicuous; achenes 8-11 mm. long, 1.5-2 mm. wide, linear-oblong, blackish, minutely puberulent and tuberculate, obscurely many-sulcate; pappus obsolete or consisting of 2 erect or squarrose rudiments. Chromosome number, $n = 17$.

Of uncertain extent (the only exact locality being that of *Melchert & Sorensen* 6240 below), on dry ledges and cliffs 5500-6500 ft. in the vicinity of Querétaro City, Querétaro, México. Flowering Aug. Map 3, closed triangle.

MEXICO. QUERETARO: *Arsène* 10083 (US); 5 mi. N. of Ciudad Querétaro along route 57, 150 yds. E. of highway, *Melchert & Sorensen* 6240 (IA).

On the shape and segmentation of its leaves and leaflets *Dahlia linearis* seems closely allied to *D. rupicola* and *D. foeniculifolia*. Its suffrutescent habit distinguishes it from the herbaceous *D. foeniculifolia*. From *D. rupicola*, appar-

ently its closest ally, it separates on such technical features as the size of its outer involucre bracts (5-9 mm. not 10-14 mm. long and 2-3.5 mm. not 4-7 mm. wide), the smaller diam. of its heads (3-4.2 cm. not 5-6.5 cm., including the rays) and the overall dimensions of its median leaves (12-18 cm. not 20-35 cm. long).

8. ***Dahlia rupicola*** Sorensen, sp. nov. TYPE: MEXICO: DURANGO: 11 mi. W. of La Ciudad along route 40, about 6000 ft., 5 Sep. 1966, *Melchert, Sorensen & Crawford* 6306 (Holotype: IA!).

Suffrutex, 9-15 dm. altus. Caules anni praecedentis lignosi 1.5-2 cm. diametro, lenticellis prominentibus verticaliter elongatis; caules novi 6-11 mm. diametro, glabri (et) pruinosi (que). Folia bipinnatisecta, 20-35 cm. longa, foliolis primariis 9-11, tribus paribus inferioribus manifeste petiolulatis, pinnulis alternis, pinnis basilaribus 12-18 cm. longis, libis segmentorum ultimorum 0.6-2 mm. latis, lineari-attenuatis, uninervatis, apice flexuoso-acicularibus; stipellis 8-12 cm. longis, plerumque (nonnisi) in nodis basilaribus et secundis rachidi affixis. Capitula 2-4; pedunculis 6-11 cm. longis; squamis exterioribus involucri late ovatis, acutis vel acuminatis, erectis vel leviter potentibus sub anthesi, in dorso 5-8-lineatis, marginibus anguste albo-hyalinis, 10-14 mm. longis, 4-7 mm. latis. Flores ligulati lilacini, 2.2-3 cm. longi, 7-11 mm. lati; flores tubulosi 85-109, lobis corollae reflexis sub anthesi. Achenia linearia, dilatata supra medium, 10-12 mm. longa, 1.5-2 mm. lata. Chromosomatum numerus: $n = 17$. Fig. 3.

Abundant along cliffs and rock ledges for a distance of about 8 miles from the type locality westward along route 40, Durango, México. Flowering Sep. Map 3, squares.

MEXICO. DURANGO: 16 mi. W. of La Ciudad, about 15 mi. E. of El Palmito, Sinaloa, 5800-6000 ft., 5 Sep. 1966, *Melchert et al.* 6312 (IA).

Dahlia rupicola is extremely abundant along the main east-west highway through Durango. It is not surprising that it has remained uncollected so long as most of the plants were growing in crevices of exposed cliffs 50-150 ft. above the highway and largely inaccessible either from above or below. When we first encountered this large population of the species we despaired of ever reaching any of the plants, but it was seen that some could be reached from a small ledge midway up the cliff. A cooperative effort with

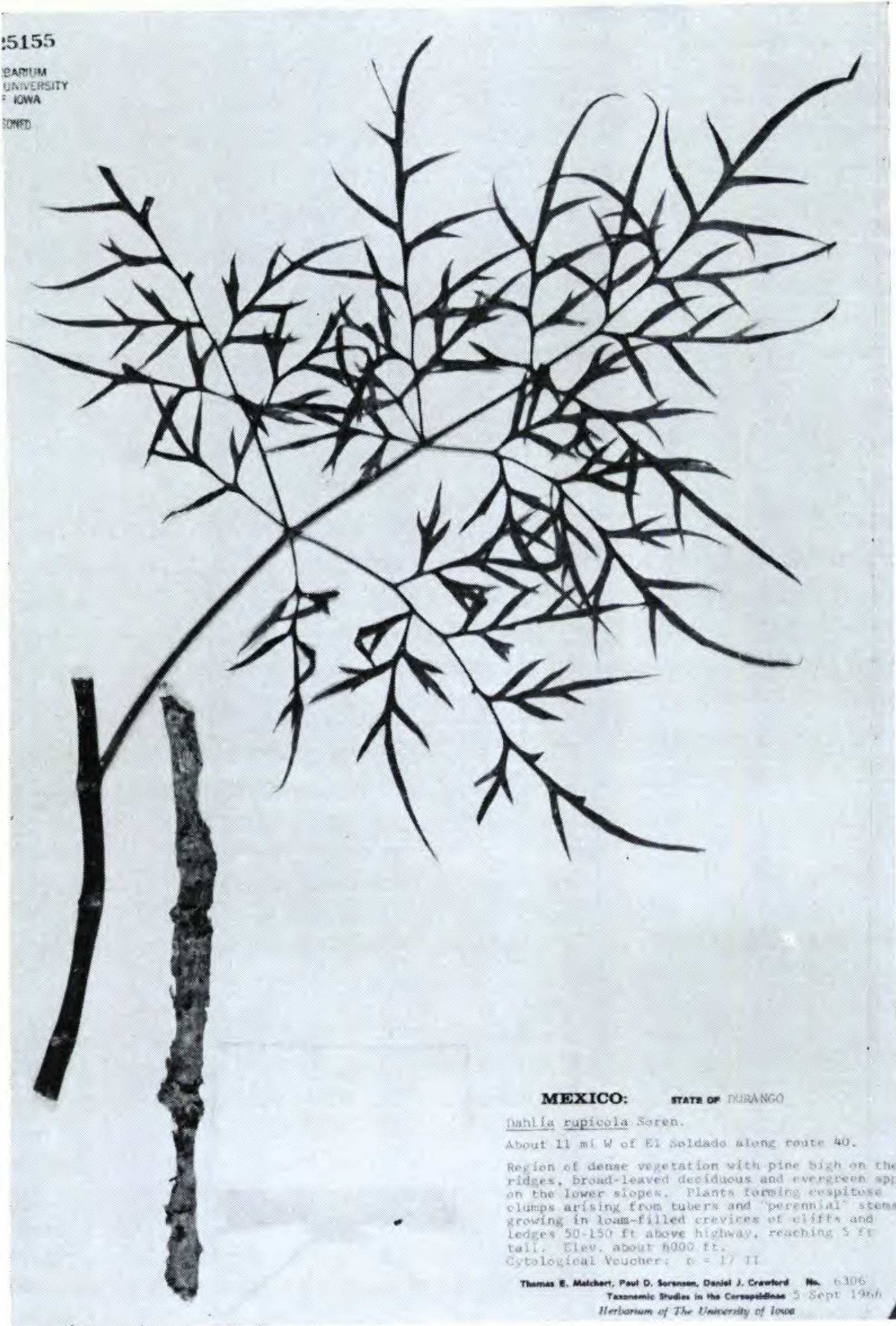


Fig. 3. *Dahlia rupicola* Sorensen. Photograph of type (IA),
 × 1/3.

one person doing the climbing and the others with binoculars in hand calling out directions from below finally succeeded. At a station farther along the highway we found a fortuitous landslide had carried down several undamaged plants which we also collected.

With one or more of the species of section *Entemophyllum* *Dahlia rupicola* shares a shrubby habit, pinnules arranged alternately on the rachilla, finely dissected leaves, a meiotic chromosome number of $n = 17$, and the presence of a white crystalline precipitate in an acidified methanolic extract of its leaves.

Dahlia rupicola most resembles *D. linearis* and *D. foeniculifolia*. These three species all have very finely dissected leaves with rather narrow and long-attenuate ultimate segments. *Dahlia rupicola* is readily distinguished from *D. foeniculifolia* by its woody habit and from *D. linearis*, its closest ally, on such technical features as the dimensions of its outer involucre bracts (10-14 mm. not 5-9 mm. long and 4-7 mm. not 2-3.5 mm. wide), the greater diameter of its heads (5-6.5 cm. not 3-4.2 cm. diam. including the rays) and its larger leaves (20-35 cm. not 12-18 cm. long).

9. ***Dahlia dissecta*** S. Wats. Proc. Am. Acad. 26: 141. 1891. TYPE: MEXICO: SAN LUIS POTOSÍ: limestone ledges, San José Pass, July 1890, *Pringle* 3167 (Holotype: US!; Isotypes: F!, GH!, ISC!, MO!, MSC!, NY!, RSA!, UC!, US!).

Freely branching perennial herb, 3-9 dm. tall, a cluster of many herbaceous stems arising from a large, horizontally-elongate ligneous tuber or rootstock, or the current season's stems branching from short (5-15 cm.) woody portions of the previous year's stems. Stems slender, terete, 1.5-4 mm. diam., glabrous, green or reddish-brown when fresh, drying to pale green or tan; internodes 1.5-16 cm. long, the upper solid, the lower hollow, the pith sometimes chambered. Principal leaves pinnate-pinnatisect to bipinnate-pinnatisect, 10-19 cm. long; primary pinnae 5-9, opposite on the rachis, the basal pinnae 2.5-10 cm. long, the pinnules alternate on the rachilla, the ultimate segments 1.0-2.5 cm. long, their lobes 0.5-9 mm. wide, broadest at the base or at the middle and abruptly tapered into a mucronate tip; margins smooth or irregularly short ciliolate, surfaces green on both sides or obscurely lighter green beneath, upper surface glossy when

fresh, glabrous or with very minute hairs along the main veins above; stipels rare or absent; petiole 2-9 cm. long, slightly flattened above; rachis glabrous or with a cluster of hairs at the rachis nodes, usually grooved above, the decurrent bases of the pinnae sometimes forming wings along the margins esp. in the terminal portions of the leaf. Heads in 2's or 3's, obliquely erect (nodding in fruit), peduncles 12-35 cm. long; outer involucral bracts erect or very slightly spreading, 5-7 mm. long, 1.8-5 mm. wide, oblong or ovate, obtuse; inner bracts 9-15 mm. long, 4-7 mm. wide; rays pale lavender to light purple, fading when dry to light or dark tan, 2-4 cm. long, 0.9-1.7 (-2) cm. wide, ovate, acute or denticulate; disc florets about 44, 6-6.5 mm. long, corolla lobes strongly recurved, yellow or yellow with purple tips, sometimes with 5 distinct dark veins; style branches about 3 mm. long, 0.5 mm. or less wide.

In the present treatment two infraspecific taxa of *Dahlia dissecta* are recognized as follows:

9a. ***Dahlia dissecta* var. *dissecta***. TYPE: MEXICO: SAN LUIS POTOSÍ: limestone ledges, San José Pass, July 1890, *Pringle* 3167 (Holotype: US!; Isotypes: F!, GH!, ISC!, MO!, MSC!, NY!, RSA!, UC!, US!).

Perennial herb, 3-7.6 dm. tall. Stems 1.5-3 mm. diam.; internodes 1.5-15 cm. long, pith rarely chambered. Leaves 10-15 cm. long; basal pinnae 2.5-5.2 cm. long, ultimate segments 1.0-1.8 cm. long, their lobes 2-9 mm. wide; petiole 2-7 cm. long. Peduncles 12-27 cm. long; outer involucral bracts 5.5-7 mm. long, 1.8-4 mm. wide, ovate, obtuse; inner bracts 9-15 mm. long, 4-6.5 mm. wide; rays 2-3.2 cm. long, 0.9-1.2 cm. wide; achenes narrowly obovate, 9-11 mm. long, 1.5-2 mm. wide, blackish, minutely tuberculate, many-sulcate; pappus absent or consisting of 2 minute rudiments. Chromosome number: $n = 17$.

Rocky slopes and ledges, 6500-8000 ft., Hidalgo and San Luis Potosí. Flowering July-Aug. Map 3, closed circles.

MEXICO. HIDALGO: Distr. of Zimapán, Barranca de San Vicente, *Moore & Wood* 4425 (NY), *Melchert & Sorensen* 6205 A-C (IA), 6213 A-D (IA). SAN LUIS POTOSÍ: San Juan del Llanos, *Halsted s.n.* (NY); arroya near San Ruizo, *Whiting* 983 (MICH).

The label on an early specimen collected by Halsted (NY) gives the locality as "San Juan del Llanos." Sherff (1955) understood this to be a reference to the town of "Llanos" in northern Puebla, shown on the American Geographic Society's millionth map. I think the small village of San Juan del Llanos in San Luis Potosí (NE. of 22° N. & 100°



Fig. 4. *Dahlia dissecta* var. *sublignosa* Sorensen. Photograph of type (NY), $\times 1/3$.

W.) is the more likely, as this locality would fall well within the known range of *Dahlia dissecta* (see Map 3).

- 9b. ***Dahlia dissecta*** S. Wats. var. ***sublignosa*** Sorensen, var. nov. TYPE: MEXICO: TAMAULIPAS: 3 mi. N. of Miquihuana in pine forest (99°47' N. Lat., 23°36' W. Long.), about 7000 ft., 14 July 1949, *Stanford, Rutherford & Northcroft* 2436 (Holotype: NY!; Isotypes: MICH!, TEX!, UC!, US!).

Herba perennis vel subherbacea 7-9 dm. alta. Caules hic annus ramificibus brevi caules (5-15 cm.) longitudinibus anni praecedentis. Folia simulans *Dahlia dissecta* var. *dissecta* autem plus grandis (11-19 cm. longa) et segmentis ultimis plus angustis (0.5-5.5 mm. latis). Pedunculis 12-35 cm. longus; involucri squamis exterioribus erectis vel effusis leviter sub anthesi, 5-7 mm. longis, 2.5-5.5 mm. latis. Flores ligulati diluti-lavanduli ad lilacini, 2.8-4 cm. longi, 1.2-1.7(-2) cm. lati; flores tubulosi flavis, 5-atronervati. Fig. 4.

Known only from the type locality and from an area 0°10' of long. W. of the type locality, 7000-8000 ft., Tamaulipas, México. Flowering July. Map 3, stars.

MEXICO. TAMAULIPAS: between Marcella and Hermosa, *Stanford et al.* 2436 A (NY, TEX, US).

On morphologic grounds the two infraspecific taxa of *Dahlia dissecta* may be distinguished by the following key:

- +Stems of the current year arising from a crown of tuberous roots or rootstock; leaves 10-15 cm. long, ultimate segments 2-9 mm. wide; outer involucre bracts 1.8-4 mm. wide. 9a. *D. dissecta* var. *dissecta*.
- +Stems of the current year branching from short (5-15 cm.) ligneous portions of the previous year's growth; leaves 11-19 cm. long, ultimate segments 0.5-5.5 mm. wide; outer involucre bracts 2.5-5.5 mm. wide. 9b. *D. dissecta* var. *sublignosa*.

In addition to the above distinctions it should be pointed out that var. *sublignosa* tends to be generally more robust attaining heights of 7-9 dm. as compared to the height of var. *dissecta* (3-7.6 dm.). There is also a considerable geographic isolation between the two taxa. *Dahlia dissecta* var. *sublignosa* is isolated from the nearest part of the range of var. *dissecta* (at San José Pass in San Luis Potosí) by about 85 miles.

Section 4. **Dahlia**. Type species: *Dahlia pinnata* Cav.

Sect. Neocaulon Sherff, Am. Jour. Bot. 38: 71. 1951.

Type species: *Dahlia coccinea* Cav.

Stems herbaceous (lignescant in *D. apiculata*) mostly with hollow internodes and septate or imperfectly septate nodes; leaves simple to 3-pinnate, pinnules opposite or sub-opposite on the rachilla (alternate on the rachilla in *D. merckii*); petioles solid (hollow in *D. merckii*); outer involucral bracts erect, spreading, or reflexed. Chromosome numbers, $n = 16, 18, \& 32$. (Species 10-27.)

10. **Dahlia merckii** Lehm. Del. Sem. Hort. Hamb. 1839; Schlectendal, Linnaea 14 (Lit.-Ber.): 130. 1840. TYPE: the original material grown in the Hamburg Bot. Gard. from seeds collected in México, the exact locality not known, *H. J. Merck s.n.* (Lectotype: GH!).

Dahlia glabrata Lindl. in Edwards Bot. Reg. 26: pl. 29. 1840. Type: based on plants cultivated in England from seed collected in México, exact locality not known, *G. F. Dickson, Esq. s.n.* Lectotype: pl. 29, Lindley, loc. cit.

Dahlia cosmaeflora Jacques, Ann. de Flore et Pom. (Jour. des Jard.) 1840: 345, pl. s.n. 1840. Lectotype: pl. facing p. 345, Jacques, loc. cit.

Dahlia decaiseana Verlot, Rev. Hort. 1864: 31, pl. s.n. 1864. Lectotype: pl. facing p. 31, Verlot, loc. cit.

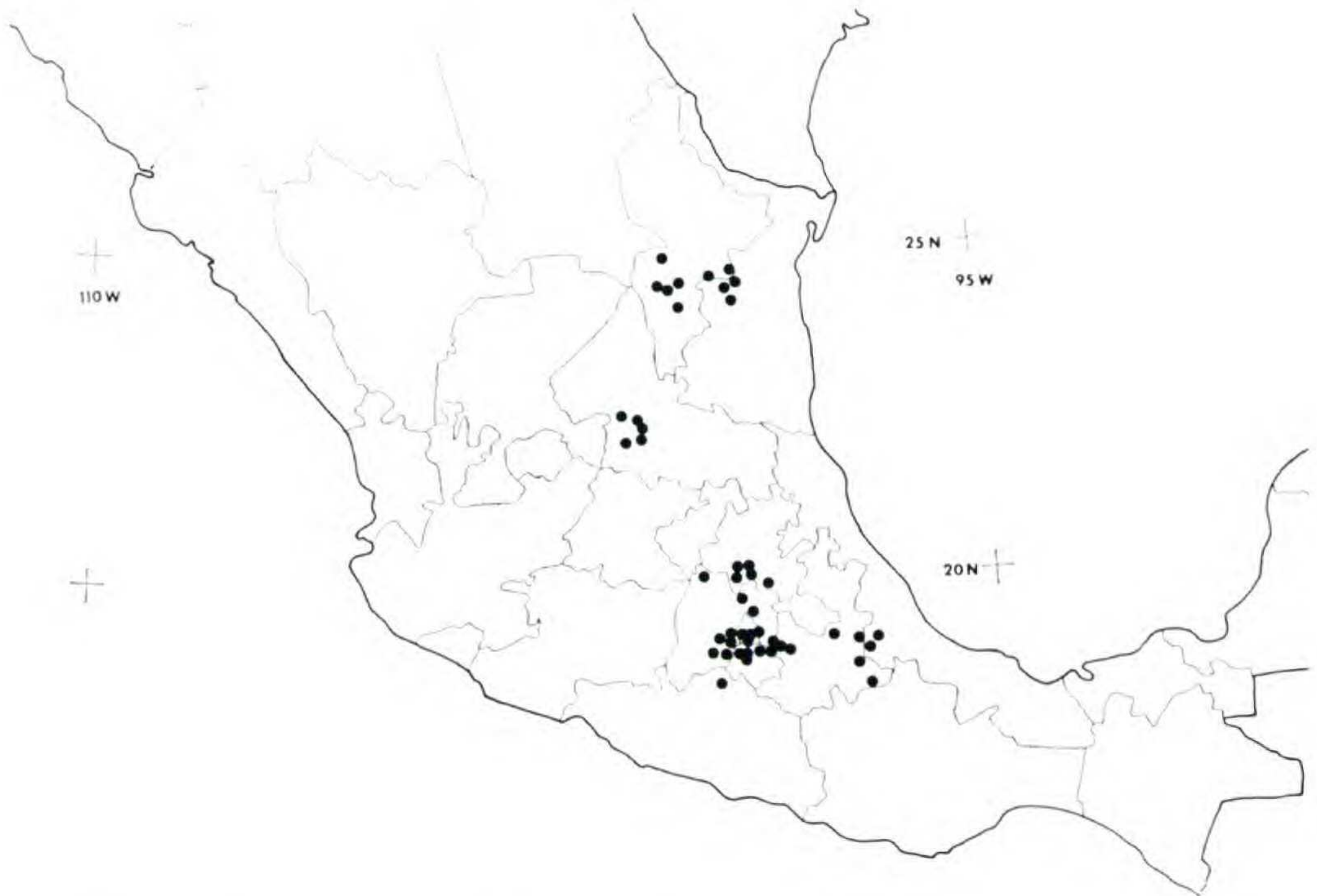
Dahlia scapigera var. *scapigera* f. *merckii* (Lehm.) Sherff, Am. Jour. Bot. 34: 141. 1947. Type: that of *Dahlia merckii* Lehm.

Herb, 4.5-18.5 dm. tall, freely branching near the base, the leafy portions averaging 1/3 to 1/2 the height of mature flowering plants. Stems 3-9 mm. diam., terete or 6-angled, sometimes strongly 6-ridged (best seen in fresh material), glabrous or sometimes a few hairs gathered at the nodes, usually red when fresh, drying to brownish-red or tan, hollow except for septa at the nodes; internodes 1-27.5 cm. long, the lower often the shortest and usually increasing in length toward the topmost and longest. Leaves once-pinnate to bipinnate-pinnatisect, 14-38 cm. long; primary leaflets 5-7, opposite on the rachis (leaflets of the secondary and tertiary ranks alternate on their rachillae), the basal pinnae 6.5-16 cm. long, sessile or stalked, the petiolules or pseudopetiolums 9-40 mm. long; ultimate segments broadly ovate to slightly obovate, 2-5.2 cm. long, 0.9-3.2 cm. wide (the length often about twice the width), the terminal segment usually somewhat larger than its companion segments; apices acute to acuminate; surfaces bicolored, lighter green beneath, the upper glabrous or sparsely pubescent, minutely appressed pubescent along the principal veins, the lower glabrous or sparingly pubescent;

margins ciliolate, the cilia now long, soft and flexuous, now short and rather stiff, irregularly serrate to dentate-crenate, 1-5 teeth per side; stipels usually present, 8-46 mm. long, 3-32 mm. wide, ovate, tips acute or acuminate, attached at each rachis node, except plants from Nuevo León and Tamaulipas on which stipels occur only at the basal rachis node or not at all (stipels sometimes also attached at the basal rachilla node); petiole glabrous, 4-16 cm. long, strongly dilated at the base, when fresh forming a conspicuous fleshy ridge around the stem, medianly terete or hemispherical, hollow; rachis glabrous except for a cluster of hairs at the junction with the primary pinnae, often U-shaped with two parallel ridges above. Heads often numerous, 10-90 per plant (fewer in material from northwest México), obliquely erect or subcernuous, elevated well above the leafy portion of stem on several to many branches, these again branched and terminated by 2-19 heads on peduncles 1-30 cm. long; outer involucral bracts spreading or reflexed at anthesis, linear to slightly spatulate, apically obtuse, 9.5-11.5 mm. long, 1.8-2.2 mm. wide; inner bracts 12-15 mm. long, 5-7 mm. wide; chaff at anthesis hyaline to yellow, sometimes suffused with purple, 4.5-9.5 mm. long, 3-6 mm. wide, enlarging in fruit to 14-18 mm. long, 6-10 mm. wide; rays whitish (said to be white on many labels) to pale lavender to purple, 2-2.9 cm. long, 1.2-2 cm. wide, broadly elliptical, acute or denticulate; disc florets 47-58, corolla yellow, yellow with purple tips or purple, 6-9 mm. long; style branches linear-lanceolate, 2.5-3 mm. long, less than 1 mm. wide; achenes more or less linear, broadest above the middle, abruptly narrowed at the top and capped by a shallow disc, 5.5-10 mm. long, 1.1-2.3 mm. wide, ventrally flattened and dorsally rounded or V-shaped in cross-section, longitudinally sulcate, dark brown to black (tan with dark speckling when immature); pappus absent or consisting of 2 minute rudiments. Chromosome number, $n = 18$.

Rocky slopes, ledges and lava fields ("Pedregales"), 6000-10,500 ft., Nuevo León and Tamaulipas in northern México, south to northern Guerrero, westward from Veracruz to western México state, frequent on cool mountain slopes of Distrito Federal, México state and Morelos. Flowering June-Oct. (Dec.). Map 4.

MEXICO. TAMAULIPAS: E. side of Cerro Linadero, *Meyers & Rogers* 2894 (F, MICH, MO, US); Cañon 4 km. W. of Miquihuana, *Stanford et al.* 767 (F, GH, MO, NY); E. & S. slopes of Cerro Peña Nevada, *Stanford et al.* 2537 (NY, TEX, UC, US); NUEVO LEON: vicinity of Galeana & Cerro Infernillo, *Mueller & Mueller* 837 (F, GH, MICH, TEX), *Taylor* 183 (F, MO, TEX); vicinity of Dulces Nombres, *Meyer & Rogers* 2894 (F, MICH, MO, US), 3009 (F, MICH, MO, US); Cerro Potosí, *McGregor et al.* 296 (MISC); along trail from Trinidad to Cerro de



Map 4. Distribution of *Dahlia merckii* Lehm.

la Cebolla, *Muller* 2879 (GH, MICH, UC); Cerro Grande, *Straw & Forman* 1389 (MICH). SAN LUIS POTOSI: without specific locality, *Parry & Palmer* 477 (GH, ISC, NY, US); slopes of Cerro Alvarez, *McVaugh* 12272 (MICH) *Palmer* 211 (F, GH, MEXU, NY, US), *Pennell* 17831 (MICH, NY); Cerro Aguilla, *Lundell* 5374 (MICH, US); 22 km. W. of Santa Catarina, *Roe & Roe* 2173 (A, WIS). HIDALGO: vicinity of Real del Monte (i.e., Mineral del Monte), *Ehrenberg* 368 (F, GH), *Mexia* 2766 (CAS, MICH, MO, NY, UC), *Martinez s.n.* (F); vicinity of Cerro de Pachuca, *Rose & Hay* 5594 (US), *Rose et al.* 8877 (US); Guerrero near Omitlán, *Martinez* 15048 (MO); along road from Pachuca to Parque Nacional el Chico, *Moore & Wood* 4105 (GH, NY); Cerro Santa Ana, NE. of Apán, *West B-18* (WIS). VERACRUZ: Loma Grande on Cerro Orizaba, *Balls* 5349 (UC, US); Maltrata at Punta de Zecatl, *Matuda S-115* (MICH), 1363 (DS, GH, MEXU, MICH, NY, US); 21 mi. W. of Orizaba along route 150, *Melchert & Sorensen* 6200 A-H (IA); Cerro Citlaltepétl, *Seaton* 277 (GH), Cambre de Acaltzingo above Orizaba, *L. O. Williams* 13496 (F). PUEBLA: La Cima near Jajalpa, *Kuntze* 23746 (NY), 23747 (NY); Cerro Tepoxuchil, vicinity of Puebla, *Arsène* 1396 (US); Los Chinos, San Manuel de la Sierra, *Balls*, B5306 (UC, US); Puente del Emperador La Venta, *Sharp* 44542 (F); 14 mi. W. of Texmelucan, *King* 3564 (MICH, TEX, UC); above Coxcatlán between Apala and summit of Cerro Chichiltepec, *C. E. Smith et al.* 3817 (F, US); along Tehuacán-Orizaba highway below Puerto del Aire, *C. E. Smith et al.* 3924 (F, MEXU, NY, US).

MEXICO: along route 190 between México City and Puebla, mostly in the vicinity of Río Frío, *Iltis et al.* 1093 (WIS), *Matuda* 21453 (MEXU, NY), *Melchert & Sorensen* 6149 A-G (IA), *Rock M-351* (TEX), *Sharp* 44100 (F), *Sharp & Gilly* 46 (MICH); vicinity of Amecameca along road to summit of Volcán Popocatepetl, *Balls* 5157 (US), *Beaman* 2040 (MEXU, MISC), 2113 (GH, MISC, UC, US), *Purpus* 1553 (POM, UC), *Urbina s.n.* (MEXU); vicinity of Huehuetoca, *Gold & Eheberle* 21770 (MEXU, US), *Matuda* 29070 (MEXU, NY); Mtns. near Guadalupe, *Bourgeau* 802 (or 862) (GH, US); along route 57, México City to San Juan del Río at k-167, *Hawkes et al.* 1395 (F); Cerro de Trancapantla, *Matuda* 21685 (NY); Cerro de Jocotitlán, *Matuda* 31003 (MEXU); 2.5 mi. S. of Tenango along route 55, *Melchert & Sorensen* 6121A & 6121-POP (IA); 26 mi. W. of México City along route 15, *Melchert & Sorensen* 6238 A-E (IA); 55 km. SE. of México City, *Weaver* 743 (GH, US). DISTRITO FEDERAL: on pedregal (lava fields) along route 95 between México City and Cuernavaca, *Clark* 7277 (MO, NY), *Manning & Manning* 531050A (GH), *Miranda et al.* 2258 (F, GH, MICH, TEX), *Melchert & Sorensen* 6104 (IA), *Ortenburger et al.* 16M732 (F), *Powell & Edmondson* 743 (MICH, TEX), *Rusby* 377 (NY, US); lava fields on the slopes of Cerro Ajusco, *Harshberger* 118 (BH), *Iltis et al.* 143 (WIS), *Matuda* 19169 (MEXU, US), *Rose et al.* 9258 (GH); slopes of Volcán Xitle, *Matuda* 19589 (MEXU, NY). MORELOS: precipitous slopes near Parque Nacional de Zempoala, *Melchert & Sorensen* 6106 (IA), *Ugent & Flores* 1484 (WIS); lava fields above Cuernavaca, *Matuda* 21476 (MEXU, NY), *Pringle* 13039 (CAS, F, GH, MICH, US). GUERRERO; Cuernavaca to Taxco, *Chute M-90* (MICH).

Sherff (1947, 1955 & 1959) reduced *Dahlia merckii* to the rank of "forma" under *D. scapigera* var. *scapigera*, explaining that this taxon was "best recognized as a somewhat localized color-form [i.e., with purple disc corollas] of *D. scapigera*" (see Table 2). This interpretation was based on his otherwise broad concept of *D. scapigera* (q.v.) proper for which the majority of the specimens he cited possessed yellow disc corollas. I have observed that the purple color of the disc florets mentioned by Lehmann (ex Schlechtendal, 1840) is a localized color-form but one which varies in its intensity and in the amount of the corolla tube so colored from plant to plant within a population. The same sort of variation has been seen in other *Dahlia* species in three of the four sections, notably *D. australis*, *D. scapigera*, *D. imperialis*, and *D. dissecta*.

Aside from its unique chromosome number, $n = 18$, *Dahlia merckii* combines several characteristics which dis-

tinctly set it apart from the remaining species. These are the alternate pinnules, hollow petioles, compact and greatly branched growth of the vegetative portion of the plant, red stems, smooth texture of its leaves, conspicuous stipels, and its large number of flowering heads on compound peduncles. The occurrence of alternate pinnules on the leaves of *D. merckii* could cause confusion with the species of section Entemophyllon, the leaves of which all possess this character. *D. merckii* may be distinguished from them by its hollow petioles and by its spreading or reflexed (not ascending or erect) outer involucral bracts.

11. ***Dahlia apiculata*** (Sherff) Sorensen, comb. & stat. nov.

TYPE: MEXICO: PUEBLA: Tlanislotepc, 7000-8000 ft., July 1909, *Purpus* 3850 (Holotype: UC!).

Dahlia scapigeroides var. *apiculata* Sherff, Am. Jour. Bot. 34: 145. 1947. TYPE: that of *Dahlia apiculata*.

Suffruticose perennial. Stems of the previous year solid or hollow, 3-6 mm. diam., purplish-gray, pruinose, glabrous, longitudinally wrinkled, lenticels conspicuous; stems of the current year 2.5-3 mm. diam., solid, longitudinally striate, glabrous except for a cluster of brown hairs at the nodes; median internodes 1-5 cm. long. Leaves once-pinnate, 7.5-14 cm. long; leaflets 5-9, basal pinnae 2.5-4.5 cm. long, 1-2 cm. wide, lanceolate, acute; surfaces glabrous except for a line of minute hairs along the main vein above; margins lacking cilia, sharply serrate with 1-4(-5) apiculate teeth per side; stipels absent; petiole 2-4 cm. long, crescent-shaped in cross-section, puberulent above in the longitudinal groove; rachis glabrous except for a cluster of hairs at the junctions with the pinnae. Heads obliquely erect at anthesis, mostly solitary, sometimes in 2's and 3's, on peduncles 8.5-17 cm. long; outer involucral bracts reflexed at anthesis, 12-17 mm. long, 3-5 mm. wide, oblanceolate, acute, 5-8-lined, usually glabrous, sometimes minutely puberulent on ventral surface; inner bracts 13-20 mm. long, 4-8 mm. wide, ovate-lanceolate, obtuse to subacute; chaff (in fruit) tan, about 20 mm. long, 6-8 mm. wide, ovate, obtuse; rays purple (fide *Purpus* 3112, MO), 3.5-5 cm. long, 2-2.7 cm. wide, ovate, acute or denticulate; disc florets yellow; achenes (immature) 9-10 mm. long, 2-2.2 mm. wide, oblanceolate or spatulate, pappus obsolete or consisting of 2 minute rudiments.

Rocky slopes at 7000-8000 ft. in the vicinity of its type locality near the border of Oaxaca and at about 5000 ft. in the Cañon del Tomellin and Amaloyán, Oaxaca. Flowering May-Dec. Map 5, stars.

MEXICO. PUEBLA: Coscomates and Los Naranjos, vicinity of San Luis Tultitlanapa near border of Oaxaca, *Purpus* 3112 (DS, F, GH, MO, NY, UC, US). OAXACA: Almaloyas [Amaloyán] at Santa Caterina, 1000 m. *Conzatti* 1647 (F); Tomellin Cañon, *Pringle* 5660 (GH, MICH, US); Almaloyán, *Seler* 1395 (GH, MO).

Sherff (1947) first described *Dahlia apiculata* as a variety of *D. scapigeroides*. He presumably based this alliance on such similarities as: (1) their woody habit, (2) their manner of producing short, leafy shoots with the leaves crowded near the base, and (3) their scapose flowering heads. Despite such similarities, however, these taxa are apparently not closely related. In the present treatment, *D. scapigeroides* is allied with the members of the newly created section Entemophyllon. This change is based on a number of characteristics which it shares with the members of that group. With this realignment *D. apiculata* remains the only lignescent member in the section Dahlia.

It may be observed from the list of specimens cited above that *Dahlia apiculata* is known from just two localities. The first is that of the type in Puebla and the other from a location 30 mi. to the south in Oaxaca. Plants collected in each of these geographic areas are seen to be somewhat distinct morphologically. The specimens collected in Oaxaca generally display fewer (3 not 5) and slightly larger (5-8 cm. not 2.5-4.5 cm. long) leaflets than those from the type locality. Both groups do, however, share the suffrutescent habit noted above. Furthermore, the leaves of the two groups are alike in their smooth texture, absence of stipels and eciliolate margins. Additional material of this species with more extensive notes on height, habit, and chromosome number is much to be desired.

12. ***Dahlia cardiophylla*** Blake & Sherff in Sherff, Field Mus. Publ. Bot. 11: 453. 1936 (a new name for *Coreopsis cordifolia* Sessé & Moc). TYPE: MEXICO: GUERRERO: mts. of Tixtla, Aug. 1787-1804 (exact date not known), *Sessé, Moçño, Castillo & Maldonado* 4027 (Holotype: MA, photo. F!).

Coreopsis cordifolia Sessé & Moc. Pl. Nov. Hispan. 147. 1890. & ed. 2. 137. 1893. TYPE: as for *Dahlia cardiophylla* Blake & Sherff

above non *Coreopsis cordifolia* (Schtz.-Bip.) Drake del Cast. Ill. Fl. Ins. Mar. Pacif. 208. 1890; Fl. Polyn. Franc. 109. 1892. which is based on *Bidens cordifolia* Schtz.-Bip. Flora 39: 361. 1856.

Herb, 7-12 dm. tall, unbranched except in the flowering portions. Stems 3-9 mm. diam., terete, many-sulcate, glabrous, stramineous or green; internodes 5-6.5 cm. long. Leaves simple, sessile and cordate-clasping, their bases slightly connate, 4-8.5 cm. long, 4-8.5 cm. wide; surfaces glabrous throughout, conspicuously bicolored, the upper dark green, the lower glaucous green, the principal veins noticeably stramineous; margins eciliolate, coarsely serrate or dentate with 5-8 teeth per side. Heads solitary or in 2's or 3's, erect or obliquely erect at anthesis, on peduncles 3-6 cm. long; outer involucre bracts reflexed at anthesis, 5-8 mm. long, 2.5-5 mm. wide, broadly obovate or spatulate, obtuse, green, glabrous, dorsally one-several-nerved; inner bracts 1-1.5 cm. long, 4.5-6 mm. wide, greenish-yellow; chaff yellow; rays spreading, 1-1.4 cm. long, 6.5-8 mm. wide, ovate, acute or denticulate, deep purplish-scarlet when fresh, drying to blackish-purple; disc florets yellow; achenes not seen. Chromosome number, $n = 16$.

Precipitous, open or lightly-wooded, rocky slopes, 5500-6000 ft., mts., vicinity of Tixtla, Guerrero, México. Flowering Aug.

MEXICO. GUERRERO: 8 mi. E. of Tixtla along new road to Chilapa at point where road crosses Barranca de Honda, *Melchert & Sorensen* 6142 A-K (IA).

Dahlia cardiophylla is a rather rare and interesting species which, until recently, has apparently not been collected, since Sessé *et al.* botanized in México (1787-1804). Its leaves (simple, sessile and cordate-clasping) are quite distinct from any other known species. In only one other species, *D. purpusii*, are the leaves believed to be exclusively simple, but in this species the leaves are rounded or narrowed (not cordate-clasping) at their base, and they are sometimes short petiolate.

13. ***Dahlia purpusii*** Brandg. Univ. Calif. Publ. Bot. 6: 76. 1914. TYPE: MEXICO: CHIAPAS: Cerro del Boqueron (now probably Cerro Ovando), Sep. 1913, *Purpus* 6680 (Holotype: UC!; Isotypes: GH!, MO!, NY).

Herb (probably perennial) at least 4 dm. tall. Stems 4-6 mm. diam. many-striate, stramineous, glabrous; internodes 3.5-11 cm. long. Leaves simple, elliptical or almost ovate, short acuminate, base tapered and slightly rounded, 8-12 cm. long, 4-7 cm. wide, sessile or very short petiolate; petiole, if evident, 1-3 mm. long; surfaces glab-

rous, slightly bicolored, salient veiny and lighter green beneath, margins eciliolate, serrate-crenate, 10-18 teeth per side. Heads solitary or in 2's and 3's, erect or obliquely erect on peduncles 5-8.5 cm. long; outer involucre bracts reflexed at anthesis, 8-12 mm. long, 3-4.5 mm. wide, ovate-lanceolate to obovate, acute or obtuse, glabrous, dorsally many-lined and sometimes reticulate veiny; inner bracts 14-15 mm. long, 5-8 mm. wide; rays probably purple, about 3 cm. long, 10-13 mm. wide, ovate, acute or denticulate; disc florets probably yellow; mature achenes not seen.

Known only from the type locality. Flowering September.

Specimens of the type collection of *Dahlia purpusii*, apparently the only ones in existence, are somewhat inadequate. None of the specimens is complete and the labels lack information on the habit of the plants. For these reasons the accompanying description must be considered provisional. Despite the scant material available the validity of this species is not questioned. Its simple leaves are quite unlike those of any other *Dahlia*. The only other simple-leaved species is *D. cardiophylla*, but the leaves of that species are sessile and cordate-clasping (not rounded or narrowed at the base).

14. ***Dahlia pinnata*** Cav. *Icones et Descr. Pl.* 1: 57, *t.* 80. 1791. TYPE: exact place of collection and date not known; originally described by Cavanilles from plants cultivated in the Royal Botanic Gardens, Madrid, from seed collected in México and sent to Spain by Vincente Cervantes, ca. 1789 (Lectotype: *t.* 80, Cavanilles, *loc. cit.*⁴).

Georgina purpurea Willd. *Linn. Sp. Pl.* ed. 4. 3: 2124. 1803. Type: based on *Dahlia pinnata* Cav.

Dahlia sambucifolia Salisb. *Parad. Lond.* *t.* 16. 1805. Lectotype: *t.* 16 in Salisb. *loc. cit.*

Dahlia pinnata var. *nana* Geo. Jackson in Andrews *Bot. Repos.* 7: *pl.* 483. 1807. Lectotype: *pl.* 483 in Andrews, *loc. cit.*

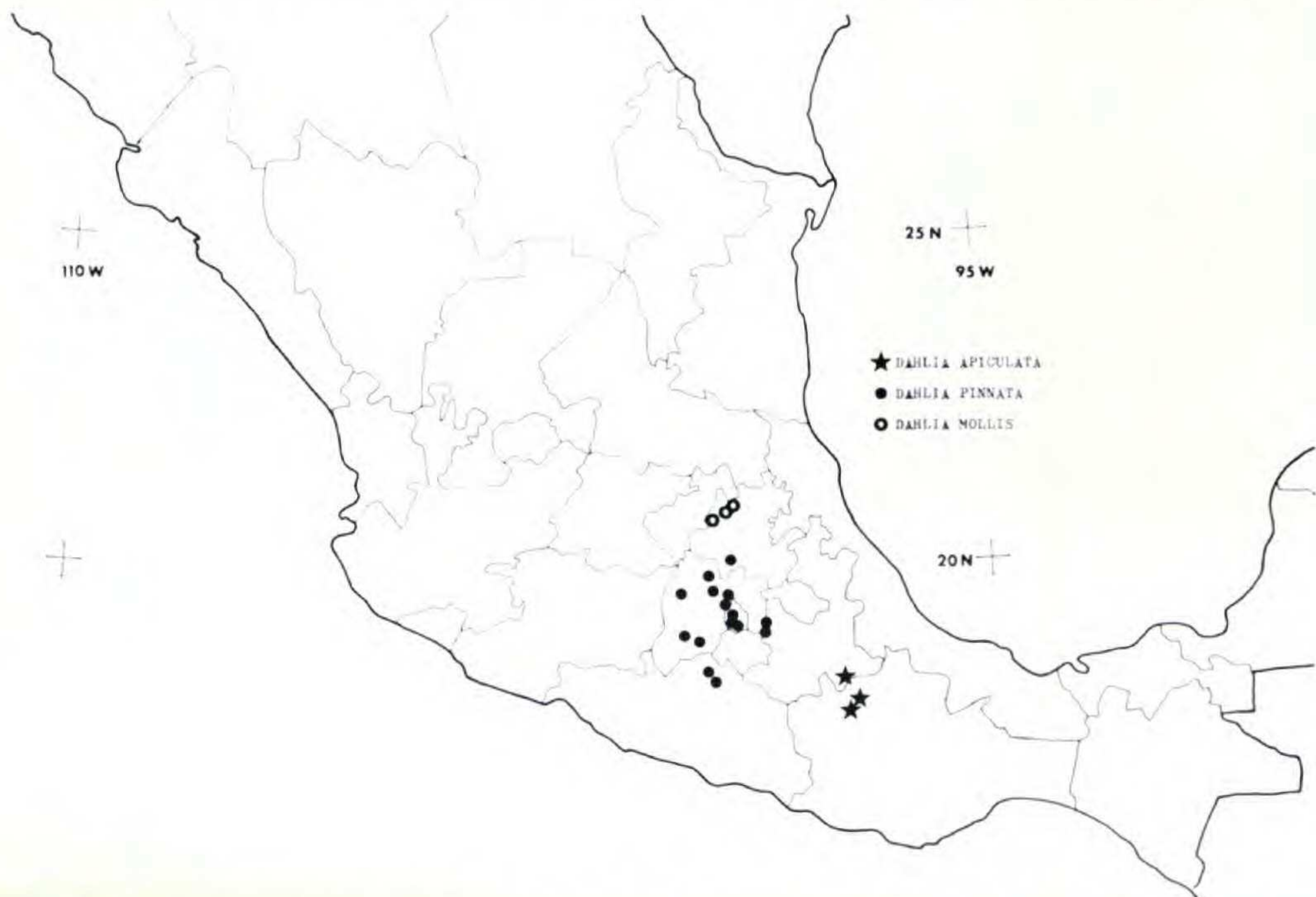
⁴In a personal communication, Dr. J. H. Beaman, Michigan State University, informs me that he made a deliberate search for the type of *D. pinnata* when he visited the herbarium of the Royal Botanic Gardens, Madrid, Spain, in 1963, but was unable to locate it. Types of other species described by Cavanilles were there indicating that had a type been preserved it would have been kept at MA.

- Georgina variabilis* [var.] *lilacina* Willd. Hort. Berol. 2: pl. 94. 1809.
Lectotype: pl. 94, Willd. loc. cit.
- Georgina variabilis* [var.] *pallida* Willd. *Ibid.* pl. 95. Lectotype: pl. 95, Willd. loc. cit.
- Georgina variabilis* [var.] *purpurea* Willd. *Ibid.* pl. 93. Lectotype: pl. 93, Willd. loc. cit.
- Georgina superflua* α *rubra* DC. Ann. Mus. Hist. Nat. Paris. 15: 310. 1810. Type: based on *Georgina variabilis* [var.] *purpurea* Willd. (G-DC, microfiche libraries A-GH).
- Georgina superflua* β *purpurea* DC. *Ibid.* Type: based on *Dahlia pinnata* Cav. (G-DC, microfiche libraries A-GH).
- Georgina superflua* γ *lilacina* (Willd.) DC. *Ibid.* Type: based on *Georgina variabilis* [var.] *lilacina* Willd. (G-DC, microfiche libraries A-GH).
- Georgina superflua* δ *pallida* (Willd.) DC. *Ibid.* Type: based on *Georgina variabilis* [var.] *pallida* Willd. (G-DC, microfiche libraries A-GH).
- Georgina superflua* ϵ *flavescens* DC. *Ibid.* 311-312. Lectotype: based on plants obtained from seed of *Georgina superflua* γ *lilacina* (Willd.) DC. (G-DC, microfiche libraries A-GH).
- Dahlia purpurea* Poir. Lam. Encycl. Suppl. 2: 444. 1812. Type: based on *Georgina purpurea* Willd.
- Dahlia superflua* (DC.) Ait. f. Hort. Kew. ed. 2. 5: 87-88. 1813. Type: based on *Georgina superflua* [vars.] DC.
- Coreopsis georgina* [var.] *nuda* Cass. Dict. Sci. Nat. 18: 442. 1820. Type: based on *Georgina superflua* DC. and *Georgina variabilis* [vars.] Willd.
- Dahlia variabilis* (Willd.) Desf. Cat. Pl. Horti Paris. ed. 3. 182. 1829. Type: based on *Dahlia pinnata* Cav. and *Georgina variabilis* [vars.] Willd.
- Dahlia pinnata* var. *variabilis* (Willd.) Voss in Vilmorin's *Blumengart.* 1: 489. 1894. Type: based on *Dahlia pinnata* Cav. and *Georgina variabilis* [vars.] Willd.
- Perennial herb, 10-18 dm. tall, usually unbranched except in the flowering portion. Stems 8-12 mm. diam., scabrous, often rather red or maroon; internodes 9-16 cm. long, hollow. Leaves simple or pinnatisect to bipinnate, coarse-textured, 13-25 cm. long; leaflets 3-5, the basal pinnae (or basal segments) 5.5-13 cm. long, 4-8 cm. wide, ovate elliptical, acute; surfaces sparingly pubescent or strigillose, ventrally the hairs short and stiff, esp. along the veins, dorsally the hairs softer, flexuous, following the principal veins; margins ciliolate, the cilia very stiff, coarsely serrate or more commonly dentate, sometimes lacerate; stipels rare, tending to occur with greater regularity on bipinnate leaves; petiole 3.5-12 cm. long, or leaves with a broadly-winged midrib, then pseudopetiolate, often pubescent on the back, broadly crescent-shaped in cross-section; rachis of compound leaves often winged with the decurrent bases of the distal primary pinnae.

Heads few, 2-8 per plant, occurring in 2's ad 3's, erect or obliquely erect at anthesis, on peduncles 5.5-11 cm. long; outer involucral bracts reflexed at anthesis, 10-14 mm. long, 4.5-8 mm. wide, obovate, acute, glabrous, dorsally several-lined; inner bracts 15-21 mm. long, 6-10 mm. wide; rays light-purple or lavender-purple often with a yellowish or rosy spot at the base, spreading, 3.8-4.2 cm. long, 1.7-2.6 cm. wide, ovate, acute or denticulate; chaff resembling the inner bracts, pale yellowish drying to tan; disc florets 96-144, mostly yellow, sometimes with light-purple veins, corolla lobes spreading at anthesis, the tube 9-11 mm. long, style branches 4-5 mm. long, less than 1 mm. wide, linear-lanceolate, long-attenuate; achenes 11-13 mm. long, 2-3 mm. wide, linear-oblongate, slightly appressed pubescent near base. Chromosome number, $n = 32$.

Rocky slopes, 7000-10,000 ft., southern Hidalgo south to northern Guerrero, west from the México-Puebla border at Volcán Popocatepetl to western México state, frequent in the volcanic mountains just west and southwest of México City. Flowering May-Nov. Map 5, solid dots.

MEXICO. SAN LUIS POTOSI: chiefly in the region of San Luis Potosí, *Parry & Palmer* 479 (GH, ISC, MO). HIDALGO: vicinity of Cerro de Pachuca, *Miranda* 4454 (MEXU), *Rose et al.* 8784 (US); Cerro de los Pitos, *Matuda* 21542 (MEXU). MEXICO: slopes of Río



Map 5. Distribution of *Dahlia apiculata* (Sherff) Sorensen, stars; *Dahlia pinnata* Cav., Closed circles; and *Dahlia mollis* Sorensen, open circles.

Hondo Canyon, *Matuda* 26182 (MEXU, NY), *Pringle* 3165 (F, GH, LCU, MEXU, MICH, MISC, MO, NY, RSA, UC); Amecameca, *Fisher* 197 (F, MO, US); near Huisquilnango, *Matuda* 21092 (MEXU); Cerro Jilotepec, *Matuda* 29121 (MEXU, NY); San Geronimo, Villa del Carbon, *Matuda* 29229 (MEXU, NY, US); Cerro de Azompán, Tequezquihuac, *Matuda* 31170 (US); 7 mi. S. of Tenancingo along route 55, *Melchert & Sorensen* 6125 A-D (IA); about 10 mi. W. of Atlalcomulco near small R.R. station of Bassoco, *Melchert & Sorensen* 6233 A-E (IA); about 12 mi. SE. of San Juan del Río along route 57, *Melchart & Sorensen* 6239 A-B (IA). DISTRITO FEDERAL: slopes of Cerro de Ajusco, *Pringle* 13546 (CAS, GH, MICH, US), *Pringle* 21556 (US), *Rose & Hay* 5534 (GH, NY, US); Santa Fé, *Bourgeau* 736 (GH, US); at Tizapán (near Villa Obregon), *Bourgeau* 746 (NY); Lomas de Mixcoac, *Lyonnet* 838 (US); Tlalpám, rocky hills, *Russell & Souviron* 32 (US).

Dahlia pinnata is the type species of the genus *Dahlia*. The name was based by Cavanilles on plants under cultivation in Madrid. These as seen by the plate accompanying the original description (Cavanilles, 1791), already had undergone artificial selection for heads producing multi-seriate ligules. This fact has led to widespread usage of the name *D. pinnata*, or some nomenclatural equivalent such as *Georgina variabilis* and *Dahlia variabilis*, for any "double-flowered" or otherwise unusual form originating in gardens.

As was the practice in the period, Cavanilles gathered seed from the *Dahlia* plants in his care (then numbering three species including *D. rosea* and *D. coccinea*) and sent them to various botanists and botanical institutions of Europe with which the Madrid gardens corresponded. Among those receiving seeds were the botanical garden at Montpellier, France, the Museum of Natural History, Paris, Holland House, Kensington, England, and the Royal Botanic Garden, Berlin. Following this distribution, which occurred in the years 1798-1804, Dahlias quickly entered into the horticultural trade throughout Europe. The number of double-flowered and other forms rapidly increased. Concomittant with this was an increase in the number of new names appearing in botanical and horticultural literature. By 1814, fully double-flowered forms had been developed in Louvain, Belgium (Hibberd, 1891), and in 1817,

Breiter listed more than 75 "varieties" in cultivation at Leipzig. The number of garden varieties or cultivars has never ceased to grow. In 1934, Howe (1936) states there were more than 14,000 named cultivars which had been produced in the past or were currently in the trade. All of these numerous horticultural aspects have been consistently equated by authors, from the early 1800's to the present, with the original *Dahlia pinnata*.

There is perhaps little doubt that a trace of the original *Dahlia pinnata* could have been found, were this possible at the time, in the genetic make-up of the many double-flowered Dahlias which arose in Europe during the early 19th Century. In my judgment, however, it is a mistake to name all of these *D. pinnata*. Nor should *any* single species be regarded as the basic one from which these numerous forms were selected. In 1929, Lawrence demonstrated on the basis of biochemical analysis, corroborated by my own findings (cf. discussion following systematic treatment of *Dahlia coccinea*), that the so-called garden Dahlia (designating collectively all Dahlia cultivars), a fertile tetraploid, $n = 32$, was of hybrid origin initially having come from a cross between *D. coccinea* with red or yellow ligules and one of the double-purple-flowered species. Of the two purple-rayed species of the genus known to produced double-flowered forms, *Dahlia pinnata* is the more likely to have been involved in this cross, inasmuch as the other is *D. imperialis*, a diploid, $n = 16$, and one of the "tree-Dahlias" (cf. Popenoe, 1920).

If one recognizes the hybrid nature of the garden Dahlia, the next question to consider is when did the original hybridization occur. Was the *D. pinnata* of Cavanilles already a hybrid at the time of its description, or did the hybridization which led to the subsequent development of the earliest "garden Dahlias" take place after seeds of the original material had been distributed to various botanical institutions in Europe? I am inclined to think the latter was the case. Had the seeds Cavanilles received from

México come from an interspecific cross or from a plant which had been derived previously from such a cross, involving in either case *D. coccinea* as one of the parents, they would have resulted in plants with ligule colors potentially ranging, in different individuals, from white through light and dark purple to yellows, oranges, and scarlets.⁵ Yet, the only color Cavanilles (1791) gives for the ligules is purple, "Corolla . . . feminis magna, coeruleo-rubens". (The terms "feminis magna" allude to the pistillate, but sterile, ligulate florets. Only the disc florets are hermaphroditic and fertile.)

The explanation given above for discontinuing the use of *Dahlia pinnata* as the correct name for the garden Dahlia does not solve the problem of naming the many forms now found in cultivation. It would be incorrect to designate the cultivated Dahlias as *D. coccinea* × *pinnata* as has been done often for some taxa known to be the first generation of an inter-specific cross. The development of our modern cultivars has involved repeated hybridization between existing hybrids as well as between hybrids and wild species. Because of this it is best to utilize cultivar names for all those garden forms which are not otherwise clearly selections from among the naturally occurring variants within a wild species population. Unfortunately, at the present time no key to Dahlia cultivars exists. The best means one has to identify cultivars is by making comparisons of his material with portraits and descriptions. To date the most complete list of Dahlia cultivars with descriptions relating to the characteristics of the heads is the booklet entitled *1968 Classification of Dahlias*, compiled and published jointly by the American and Central States Dahlia Societies. In this booklet the names of cultivars are alphabetically arranged within groups based on the diameter of the heads. After each name are symbols

⁵One usually expects the F₁ to be fairly uniform. Such is not the case in *Dahlia*. The great variability in Dahlia plants is due to the prevailing self-incompatibility which maintains in all progeny a rather high degree of heterozygosity.

which denote the color of the rays and the horticultural category (i.e., whether Formal, Decorative, Pompon, Collarrette, etc.). The purpose of this listing is to be able to determine the application of a name by checking the description; however, I have found it practicable to use it for the identification of an unknown by reading through the descriptions within a given group and narrowing the number of possibilities to three or four. Thereafter it becomes necessary to search out portraits for comparison in trade magazines and catalogues.

Dahlia pinnata sensu stricto, is characterized by its rather coarse, often scabrous leaves which vary in their degree of segmentation from simple and unlobed to bipinnate. The petioles, petiolules and rachises are conspicuously winged by the decurrent bases of leaflets and pinnules. The variable margins are often rather coarsely toothed, sometimes lacerate, the teeth usually protruding beyond the outlines of the blades. The variable lobing and segmentation of its leaves are in part due to environmental influence. Plants grown in the greenhouse from wild tubers collected in México (*Melchert & Sorensen* 6125 & 6233) produced simple to pinnate-pinnatifid leaves. Simple leaves developed during winter months (without supplementary illumination) and the pinnate-pinnatifid leaves developed during spring and summer months or during winter months with supplementary illumination.

The geographic range of *Dahlia pinnata* is sympatric with *D. rudis* and *D. atropurpurea*. *Dahlia rudis*, to which *D. pinnata* is closely related, is distinguished by its smooth-textured, flexible (when dry) leaves and by its much larger outer involucral bracts (15-25 mm. not 10-14 mm. long). *Dahlia atropurpurea* is distinguished from *D. pinnata* by the color of its rays which dry to a dark, almost blackish, purple and by its non-winged petiolules and rachises.

To be continued